THE UNIVERSITY OF ALBERTA

THE SPATIAL ORGANISATION OF PIKAS (OCHOTONA), AND ITS EFFECT ON POPULATION RECRUITMENT

by

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "The Spatial Organisation of Pikas (Ochotona), and its Effect on Population Recruitment" submitted by Stephen Charles Tapper in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

Home range, dispersion, and dispersal patterns of pikas were studied for three summers in S. W. Alberta.

Home ranges of adults consisted mainly of talus adjacent to areas of vegetation used for grazing. With the construction of haypiles in late summer (July - September), pikas used the central portions of these home ranges more intensively than they did in early summer (May - June). Home ranges of males were larger than those of females in early summer, but not in late summer. Home range size varied from area to area and was associated with changes in population density, and with amounts of vegetation on feeding areas.

Pika populations were organised into pairs of males and females with members of the pairs sharing much of their home range with each other, but the degree to which this occurred varied with density and season. There was little overlap between home ranges of females, whereas in males overlap was considerable in early summer but declined to about the same level as in females in late summer. Home range overlap increased at higher densities. Relative dominance between neighbouring males was apparent and some were pushed to marginal areas where they generally remained unpaired.

Dispersal of juveniles between populations occurred in animals of both sexes. Within populations, males moved little in the year of their birth, whereas females moved various distances; young males, however, were apparently forced to move again the following spring. Settlement patterns of young pikas suggested that adult females that were lost were replaced directly by dispersal of juvenile females, whereas males that were lost were replaced in spring by yearlings, or by unpaired neighbouring males.

In three years, the population on the main study area showed an increase. Most of this was due to a greater number of marginal unpaired males rather than an increase in the number of breeding pairs.

It is concluded that social behaviour affects both the number and location of new recruits settling on rock-slides, and that this sets an upper limit on the number of breeding pairs in pika populations.

ACKNOWLEDGEMENTS

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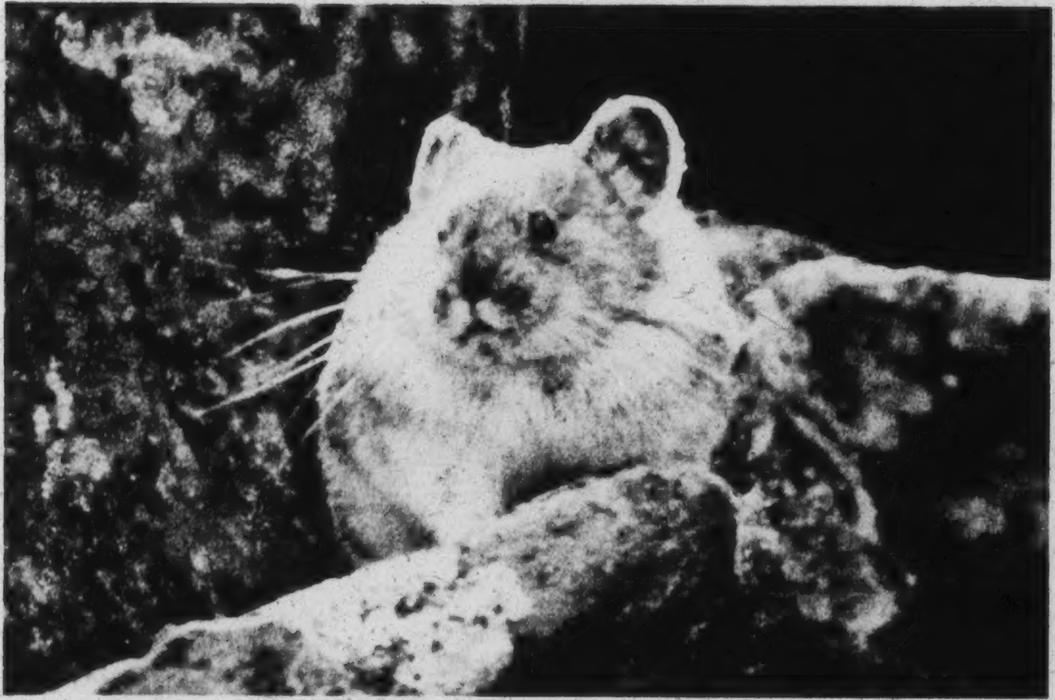


INTRODUCTION

Most vertebrate populations appear to possess some form of social organisation which not only determines the relationship of one individual to another, but also serves to organise the population in space and time. Wynne-Edwards (1962) suggested that these systems whatever their other functions may be, also serve to restrict the uncontrolled growth of the population in terms of numbers. This may be done by displacing surplus individuals or by restricting the number that breed each year. Thus, important resources such as food supply would be utilized more efficiently over the long term. Wynne-Edwards went even further and suggested that this was the primary reason for these systems developing, and defined a society as an "organisation capable of providing conventional competition."

Such an hypothesis is not readily testable with field experiments since it would require experimental manipulation of behaviour. Although this has been done to a limited extent with the injection of hormones (Watson 1970), such methods are not of wide practical use at this time. An alternative approach is to study the relationship between social behaviour and population dynamics in both undisturbed and experimentally manipulated populations, and accumulate new evidence which can be evaluated for or against this hypothesis. This was the approach used here.

Pikas (Ochotona princeps) are particularly well suited to this type of study since they are diurnal, habituate readily to humans, can be easily marked, and individuals are very local with small home ranges. This makes their behaviour relatively easy to document. However, activity under the rocks cannot be studied by direct observation, but MacArthur (personal communication) using radio-transmitters implanted into the body cavity of wild pikas had no evidence that they move more than a few metres under the rock surface. His data also agree with the observations of Krear (1965) which suggest little activity at night. Also they live in areas of restricted habitat (rock-slides) and many populations can be considered as discrete units.

The objectives of my study could be set out as two questions -

1. Do pikas have a social system which could operate as a regulatory mechanism?

2. If so, does it operate in this way?

To answer the first question it had to be shown that a form of conventional competition existed which either limited the total number of animals living within the population or restricted the number that bred. Prior to my study, there was some evidence that pikas are territorial (Kilham 1958, Broadbooks 1965, Krear 1965) and competition for space appeared likely. Therefore, a thorough documentation of spatial relationships among pikas was undertaken, so that the exact nature of any spacing system could be evaluated.

If pikas were shown to have a territorial system, a demonstration of its operation as a regulatory mechanism would require that surplus animals be shown to be displaced, at least from the breeding population. In order to do this, young animals were individually marked, and their dispersal and settlement patterns studied with respect to dispersion of adults. The settlement of young animals was observed on; (a) areas which appeared saturated with adults; (b) areas where vacancies were known to exist (established animals having died or been removed), and (c) on areas where all individuals had been removed. If territoriality was limiting the population, permanent recruitment would be expected to correspond directly with vacancies in the established population.

This study began in May 1969 and continued during the summers of 1970 and 1971, with some additional data collected in May 1972. The study populations were in the Livingstone Range of the Canadian Rockies in South Western Alberta.

STUDY AREAS

Since pikas are restricted to rockslides, the specific study areas consisted mainly of talus interspersed with vegetation. Four study sites were used, and they were designated Areas I-IV inclusive.

Areas I-III were chosen because they were discrete units of habitat all within 3 kilometres (2 miles) of each other (Fig. 1) and were at elevations between 1500-1800 metres (5000-6000 ft) in the Sub-alpine Forest Zone (Rowe 1959). The surrounding forest consisted mainly of immature lodgepole pine (Pinus contorta), and meadow areas and forest clearings were dominated by lush mixtures of grasses and herbs. These three rockslides were also inhabited by other medium-sized mammals, particularly wood rats (Neotoma cinerea), golden-mantled ground squirrels (Spermophilus lateralis), red squirrels (Tamiasciurus hudsonicus), and yellow pine chipmunks (Eutamias amoenus). Abundant carnivores were badgers (Taxidea taxus), coyotes (Canis latrans), long-tailed weasels (Mustela frenata) and short-tailed weasels (Mustela erminea).

Area IV, in a large mountain basin about 16 kilometres (10 miles) to the north of Areas I-III, was between 2300 - 2500 metres (7000-7500 ft) in elevation and just

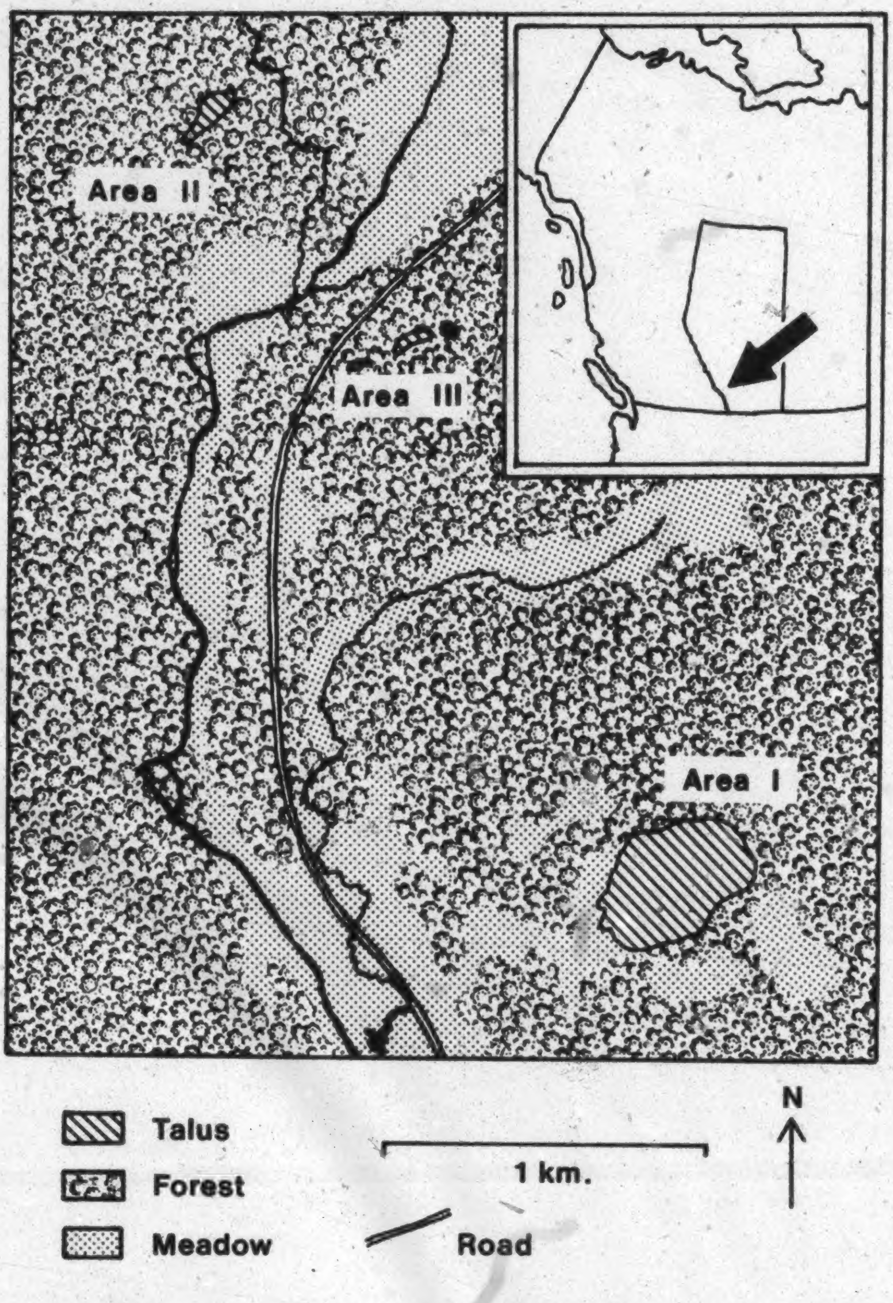

Area II
Area III
Area I
Talus
Forest
Meadow
Road
1 km.
N

Fig. 1. Map showing geographical location of study areas (inset), and their relative positions in the Livingstone River Valley.

above tree-line. The fauna was alpine in character with Eutamius minimus replacing E. amoenus, and the rocky slopes were inhabited by hoary marmots (Marmota caligata).

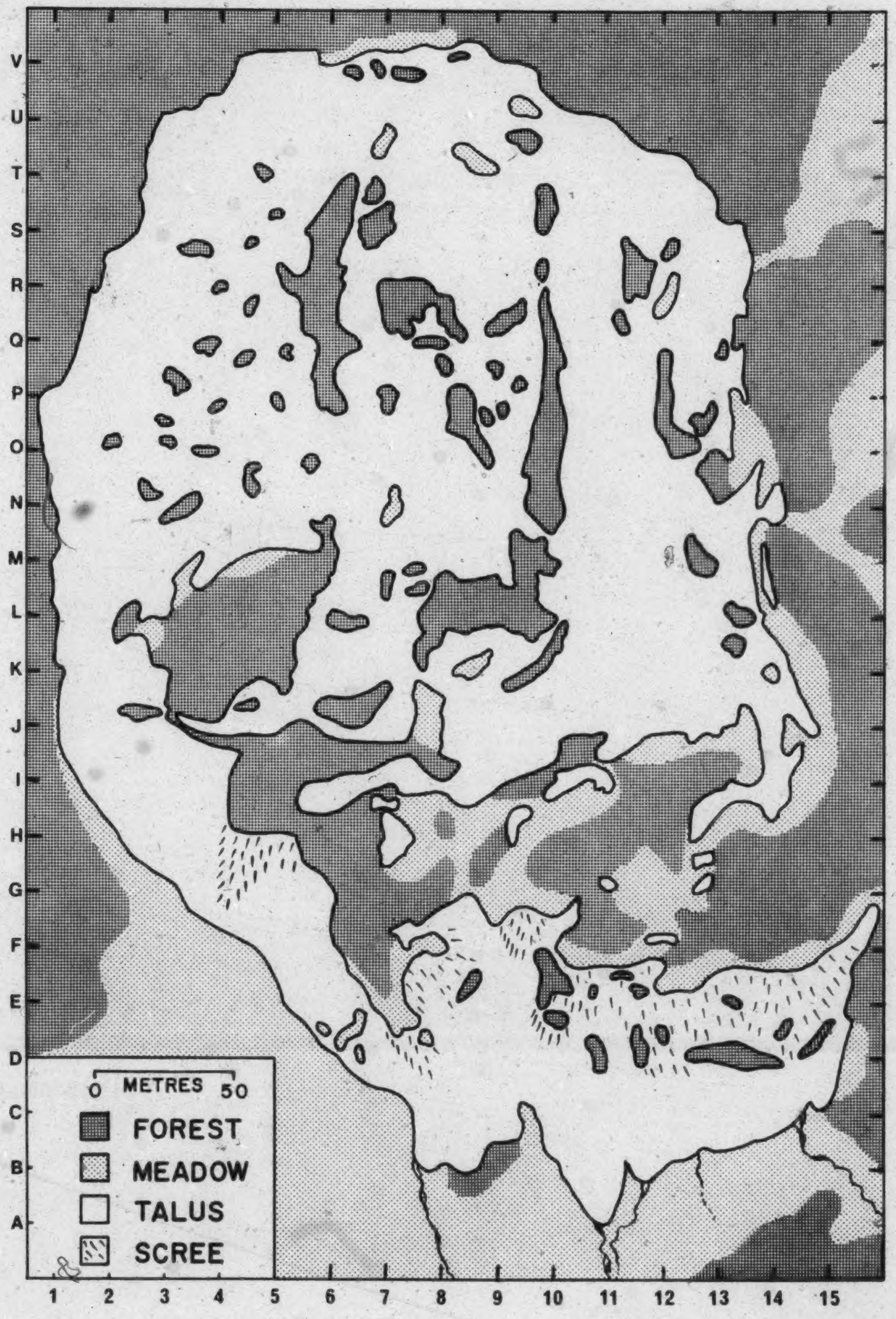
Area I

This was a large rockslide of about 10 hectares (Fig. 2). The talus, of well weathered rock with a heavy lichen covering, was interspersed with stands of lodgepole pine, and with scattered white spruce (Picea glauca) alpine fir (Abies lasiocarpa) and limber pine (Pinus flexilis). Under the forest canopy and on the upper sections of the slide the ground vegetation was sparse. The lowermost portion of the slide adjoined a meadow of plentiful grasses and herbs where springs kept the meadow moist for most of the summer.

The rockslide was situated on a slope with a mainly southerly aspect. Hence, most parts of the slide were free of snow relatively early in the year, usually by early May. Some of the upper sections of talus, where extensive drifting occurred, remained snow-covered for several weeks longer.

This area, on which most of the behavioural work was done, had an average population of 25 adult pikas, and was studied intensively for three summers (1969-71). Complete censuses were obtained in 1970 and 1971, and a

Fig. 2. General habitat types on Area I. Axes show grid of 20 X 20 metre squares.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7
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9
10
11
12
13
14
15
0 METRES 50
FOREST
MEADOW
TALUS
SCREE

good estimate of the adult population was made in 1969.

Area II

This was a small rockslide with about 1.5 hectares of talus surrounded by forest. It sloped in a westerly direction away from the base of a cliff and ground vegetation was generally sparse.

This slide had an average population of only 8 adults. Complete censuses were made during all three summers of study. All pikas were removed from it in May 1971 as part of a recolonisation study.

Area III

This area consisted of a small rockslide of about 1 hectare surrounded by mature spruce forest under which ground vegetation was very sparse. The slide sloped in a northerly direction away from the base of a cliff.

There were 8 adults here in the spring of 1971 and they were used for a replacement study in that year. The area was not used during the other years.

Area IV

This rockslide was in a large mountain basin facing generally northeast. The basin (measuring 1000 metres in length and about 500 metres in breadth) had continuous talus at the base of the surrounding cliffs. The area was not discrete since other basins adjoined to the north and south.

This population was used mainly for experimental purposes, food stores of some pikas being manipulated in 1969 (Appendix I), and one section of talus cleared of pikas in 1971, as part of a recolonisation study.

Meteorological records were not kept for each study area, but general weather changes during the study are shown in Appendix II -- these are from the Highwood River Ranger Station (6·5 kilometres north of Area IV).

METHODS

Capturing and Handling

In order to determine home ranges and population levels I used a colour ear-tagging system so that individual animals could be recognised in the field without repeated recaptures.

Galvanised metal Sherman traps (10 X 10 X 36 cm) were used for initial capture and were usually prebaited a day or two in advance with willow (Salix) and other green shoots. Traps were set in talus areas and were checked every hour, since animals tended to exhaust themselves rapidly or become overheated in warm weather.

After capture, a pika was dropped into a polythene bag and weighed. The weight of a juvenile was used to estimate the animal's age in days (Millar 1971). The animal was manipulated within the bag so that the anal region protruded through the opening and sex was determined by everting the cloaca and checking for a penis or clitoris (Duke 1951). Juveniles were often difficult to sex in this manner until they were approximately two months old, hence sexing of juveniles was often omitted until they were almost adult size. However, beginning in 1971, I attempted to sex the younger animals by classifying those which had a rounded tip to their genital organ as males, and those with a flattened tip as females. This proved fairly accurate, since of ten animals which were recaptured when larger, only one had had its sex incorrectly determined. Another criterion used to establish sex in juveniles was the 'long' call. This call is given almost exclusively by males (Krear 1965), though there is some evidence that adult females may give it, or a similar call, on rare occasions (Severaid 1955; Sharp 1973). No marked females in my study were heard to give this call. Once sex had been determined, the animal was reversed in the bag so that the head region was exposed. Two metal eartags with coloured discs were applied to each ear. Thus an animal was assigned a two colour code which was recognisable from either side. Using different colours and different positions of the tags on the ear, up to 100 animals could be distinctively marked, which was sufficient on all study areas.

Observations

Since juvenile pikas remained in the general area of the nest site prior to dispersal, it was usually possible to attribute recently emerged juveniles to a particular female.

Home ranges, dispersal movements, and a periodic census of the populations were all determined by direct observations on individually marked animals. All study areas, except Area IV were staked out in 20 X 20 metre squares, with a marked post at each point. Positions of animals were then noted relative to these stakes. In most cases it was possible to estimate an animal's position to within 3 or 4 metres. Locations were noted in the field and later plotted onto base maps of the study area, on a daily basis. Activities such as feeding, calling, and carrying vegetation were also recorded. If an animal was seen running from one location to another the movement was plotted as a line on the map. The data from these maps were later transformed into a series of individual observation points which could be represented by a number from each axis of the grid. Linear movements of animals were considered as single observation points every five metres (ie. an animal running 10 metres was considered to have been observed three times at three locations, the beginning, the middle and the end of its run). This approach enabled quantification of the data and made analysis of the spatial use of home ranges simpler.

No attempt was made to randomise either periods or locations of watching; instead every effort was made to maximise the number of observations for all individuals known to be in the population. Thus more time was spent attempting to observe animals which were seen less frequently. Hours of watching were variable but were concentrated during periods when animals were most active, which was generally morning and evening.

In making observations, an observer patrolled the study area pausing to note the activities and locations of marked animals. Most animals quickly habituated to humans and appeared undisturbed even if an observer approached to within a few metres. If animals were frightened, they usually darted out of sight beneath the talus. Hence, they were not chased out of their normal areas of activity. Most observations were made with binoculars at distances between 10 and 50 metres.

Analysis of Data

Home ranges were analysed using an IBM 360 computer. Data in the form of a matrix were entered and using a specially designed APL programme, home ranges were plotted for each animal during specified time periods. These plots showed not only the shape and extent of the home range but also intensity of use of different parts -- based on the percentage of observations in different areas. The programme also calculated the centres of activity (Hayne 1949). These home range maps were overlaid and the spatial relationships between animals studied.

Because many of the data were not normally distributed, most of the statistical analyses are non-parametric. The various tests used are described in Siegel (1956) and/or Sokal and Rohlf (1969). A probability value of ≤ 0.05 was considered significant, but actual probability levels are given where appropriate.

HOME RANGE

Concepts and Problems

Jewell (1966) reviewed many of the concepts and problems associated with home range. He restated Burt's definition of home range as follows: "Home range is the area over which an animal normally travels in pursuit of its routine activities." Burt (1943) specifically excluded dispersal, exploratory, and migratory movements from his definition. Although this is probably the commonest use of the term home range, as a definition it lacks objectivity since it is difficult to specify what activities are routine and what are not. For the purposes of this study, home range is defined as: "The area in which an individual spends all of its time, for a specified time period." Weeden (1965) used a similar definition for tree sparrows and referred to it as the total activity space.

Another problem associated with home range is a realistic method for plotting it graphically. Many methods have been used depending on the type and quantity of data analysed. Several methods which are specifically designed for use with a live trapping grid, and certain mathematical methods such as those used by Dice and Clark (1953), and Jennrich and Turner (1969), which make assumptions of circularity or bivariate normality, are ignored since they are not applicable to the type of data obtained. Perhaps the simplest method is a line surrounding all the observations or trapping points of an animal, as used by Brown (1969). A more objective adaptation is to join the most peripheral points with straight lines to form the smallest convex polygon -- as used for deer (Bramley 1970). This method has been modified to include re-entrant angles (Harvey and Barbour 1965), which eliminates some of the error developed where large areas containing no records are included.

The above methods have the advantage of being quick and easy and are generally simple to interpret. They have several major disadvantages however, two of which are: (1) they imply a specific boundary which may not exist -- in fact an animal may only be aware of a gradual decrease in its familiarity with the terrain at the edges of its range; and (2) they often enclose large areas where there are no records, which may lead to entirely false impressions of the spatial relationships among animals. Hence, these methods are not useful for looking at details of home range.

Another frequently used technique is to plot location records in the form of scattered points on a map; this is often done in observational or radio-telemetric studies, examples being Schaller (1961), Grubb and Jewell (1966), Ables (1969), and Siniff and Tester (1965). Sometimes this technique is extended to plotting runways and paths used by an animal, eg. Kaufman (1962) and Altman (1962). This method is ideal where individual animals are considered in detail, but graphically, becomes messy when several animals with overlapping ranges are plotted. Also, it is very difficult to quantify the data in terms of area without resorting to one of the earlier methods as well.

In my study an attempt is made both to characterise and quantify home ranges and the spatial relationships between animals, so that they can be analysed statistically. To do this an objective, yet reasonably realistic method was required.

The method used depicts the home range on the basis of 5 X 5 metre squares. The criterion for inclusion of a square in an animal's home range is based on the animal being observed at least once within that square during the specified time period. The 25 square metre unit was chosen as a useful size for several reasons: (1) it was a small enough distance to be easily estimated in the field (the study areas being marked with numbered stakes in 20 X 20 metre squares); (2) a reasonable graphical picture of the home range was obtained using the average quantity of data; (3) five metres seemed from casual observation to approximate the usual minimum individual distance between animals; and (4) it was the largest area which could reasonably be expected to be in the view of a pika at most times, given the nature of the terrain.

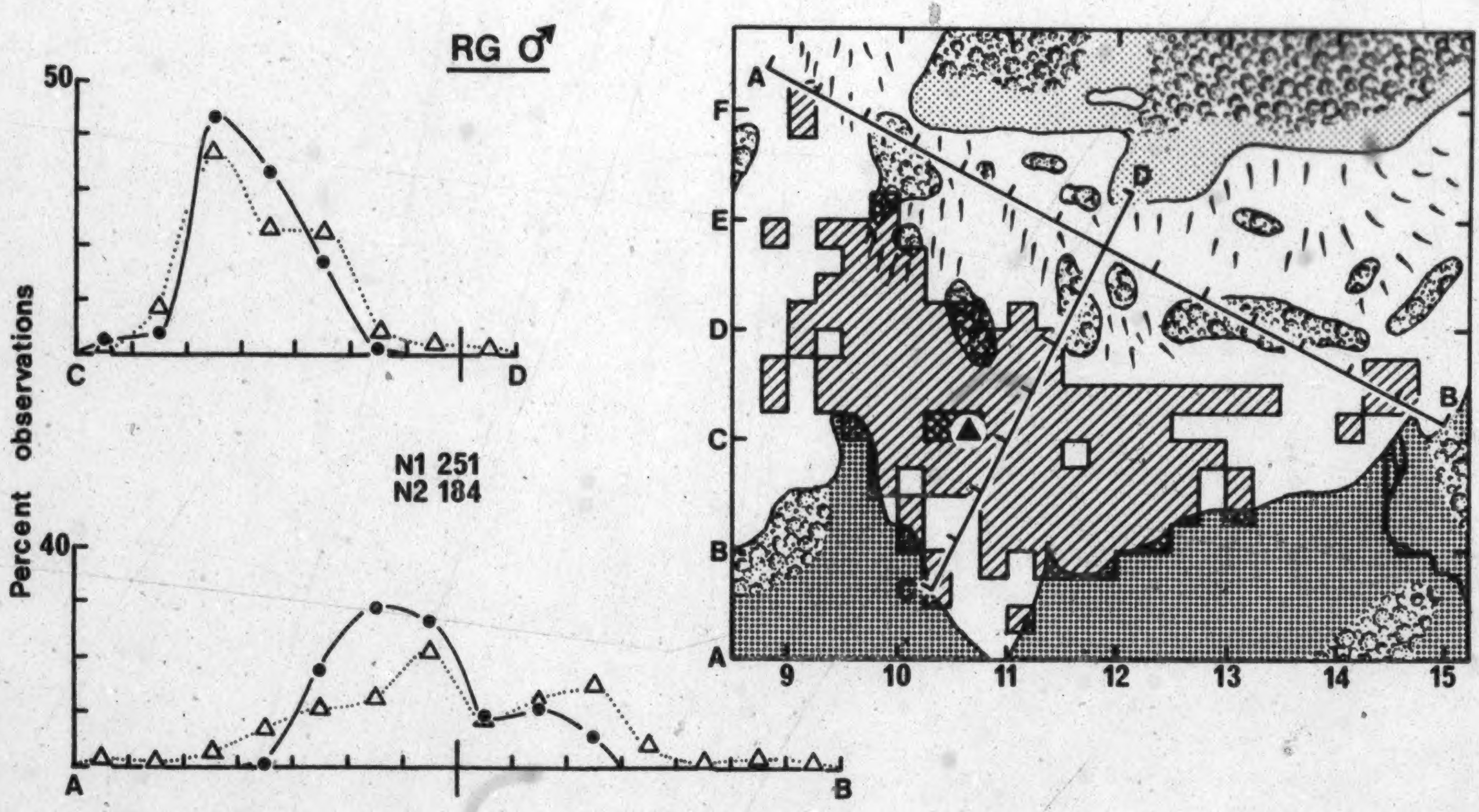
Using this method it was possible to show details of shape and use of home range, and at the same time enabled home range overlap to be measured in an objective fashion. This technique was used to establish the nature of the spatial organisation of pikas. After general spatial relationships were determined, other methods were used to show changes in dispersion pattern of the populations with time.

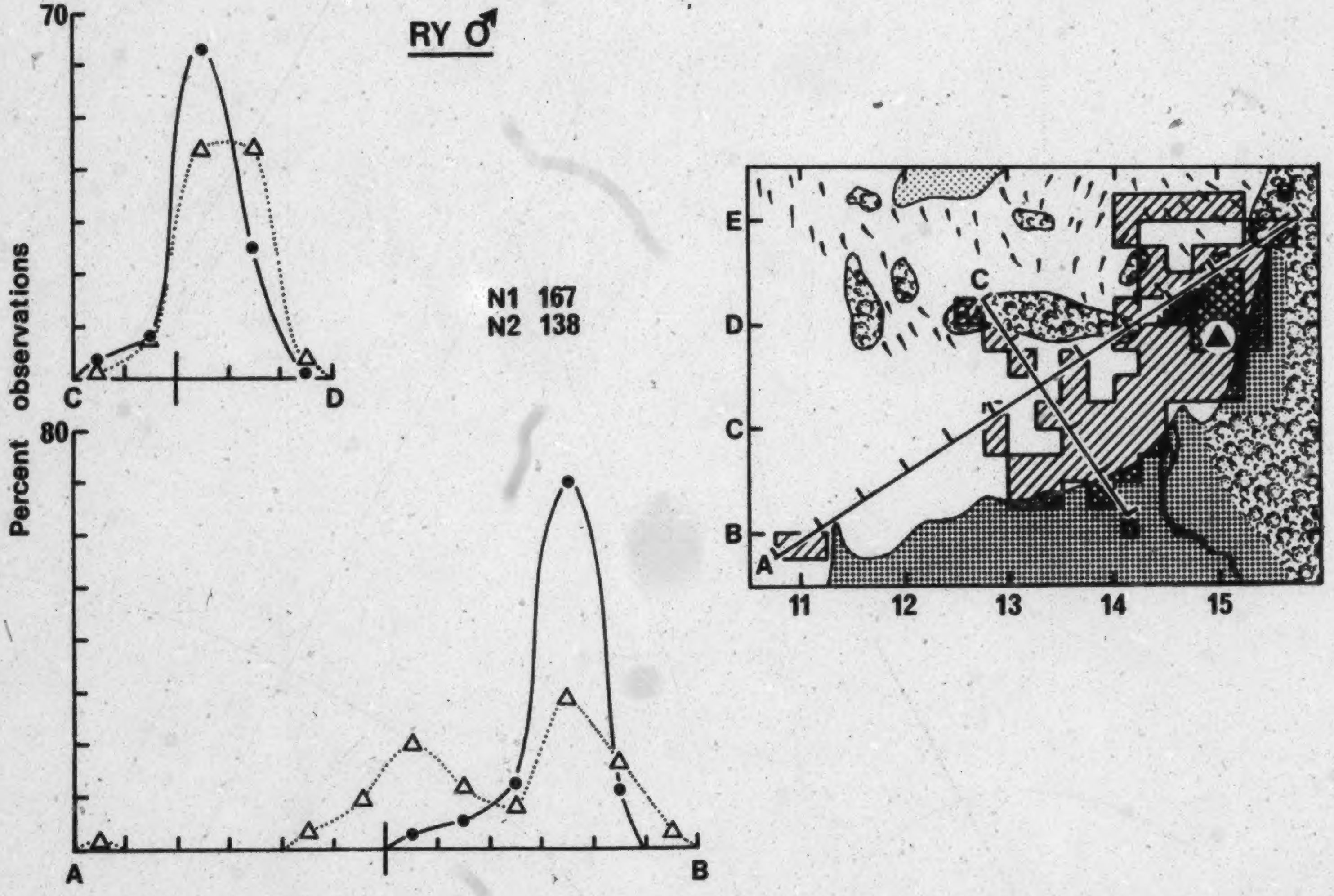
General Topography of Home Range

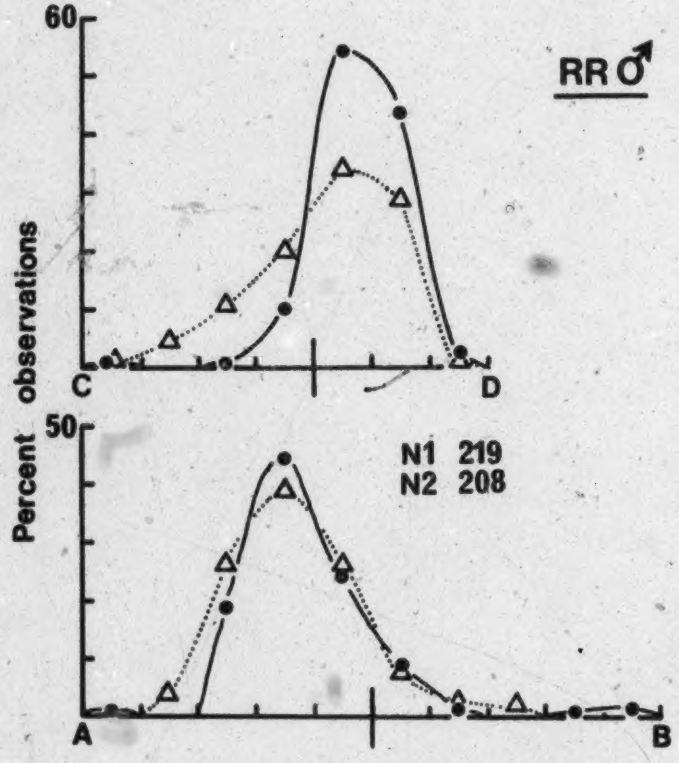
Home ranges of 10 pikas (5 males and 5 females) are shown in Fig. 3. Home ranges of pikas usually included a large area of talus adjacent to meadow areas which were used in feeding and gathering vegetation. Between July and September most of an animal's activity was concentrated around the haypile site and this area may be termed a core area (Kaufman 1962). These haypile sites were used in successive years by the same or different pikas and appeared to be fairly traditional. This

Fig. 3. Home ranges of five adult males (pp. 21-25) and five adult females (pp. 26-30) on Area I during 1970. Home ranges are drawn on the basis of 5 X 5 metre squares; co-ordinates on the maps are part of the 20 metre grid system (see Fig. 2). Graphs show intensity of use of home range along its long and short axes - these are based on the percentage of observations within each 10 metre strip at right angles to these axes (see p. 37).

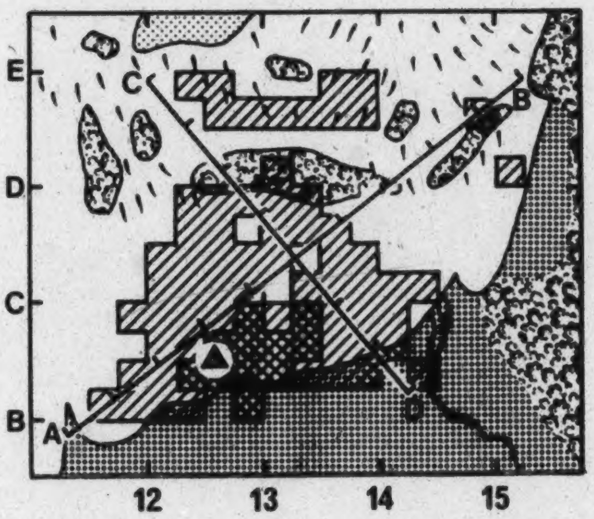
▨	Home range
▩	Home range - core area (> 3% of observations in each square)
▲	Haypile site
●	Nest site of female
▭	Talus
▧	Scree
▒	Forest
░	Sparse meadow
▦	Lush meadow
······△	May - June 1970
—●	July - September 1970
N1	Number of observations, May - June 1970
N2	Number of observations, July - September 1970.


RG ♂
50
C
D
Percent observations
N1 251
N2 184
40
A
B
F
E
D
C
B
A
9
10
11
12
13
14
15


RY ♂
N1 167
N2 138
Percent observations
70
C
D
80
A
B
E
D
C
B
A
C
D
11
12
13
14
15


60
Percent observations
C
D
50
N1 219
N2 208
A
B

RR ♂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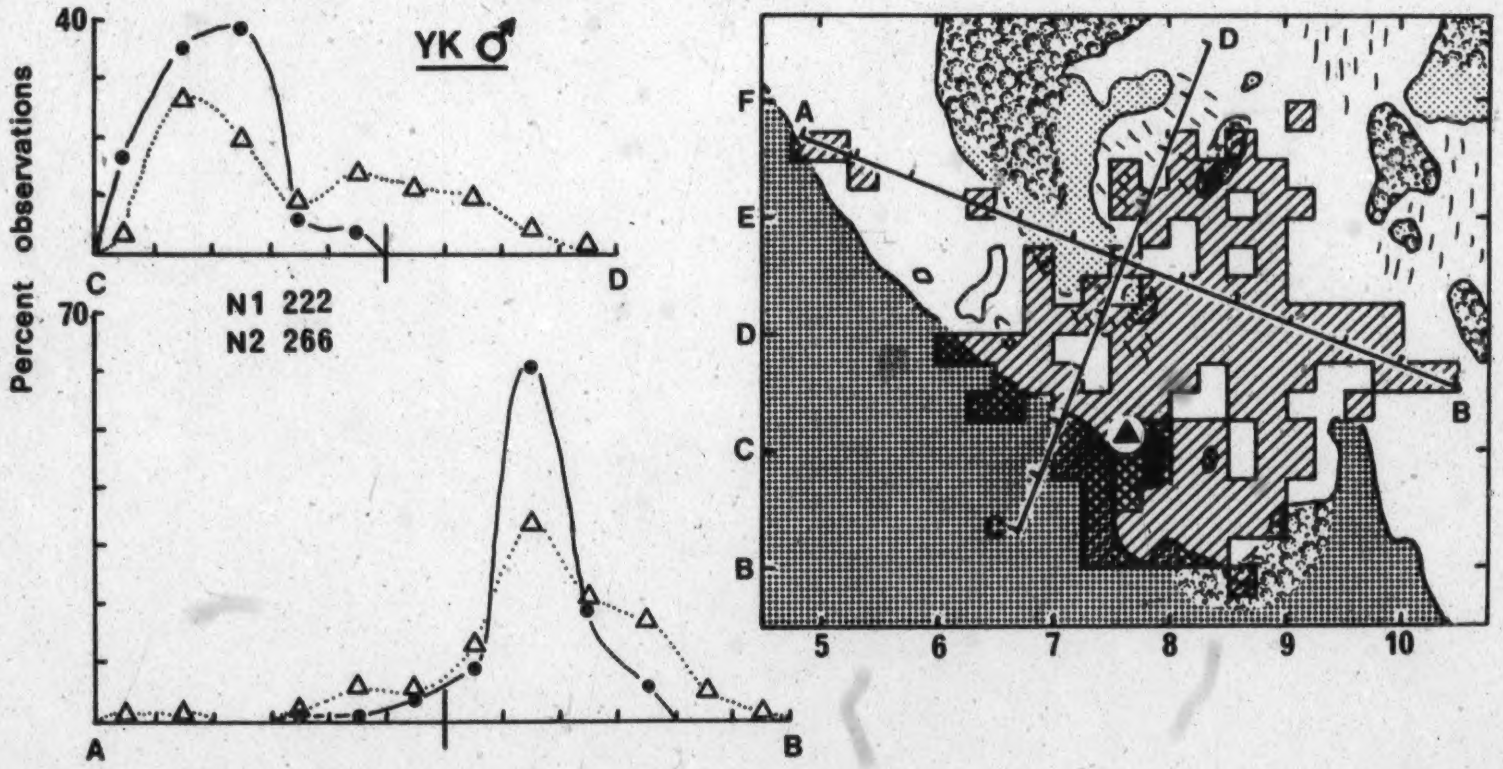
YK ♂
40
70
Percent observations
C
D
N1 222
N2 266
A
B
F
E
D
C
B
5
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8
9
10
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B
C
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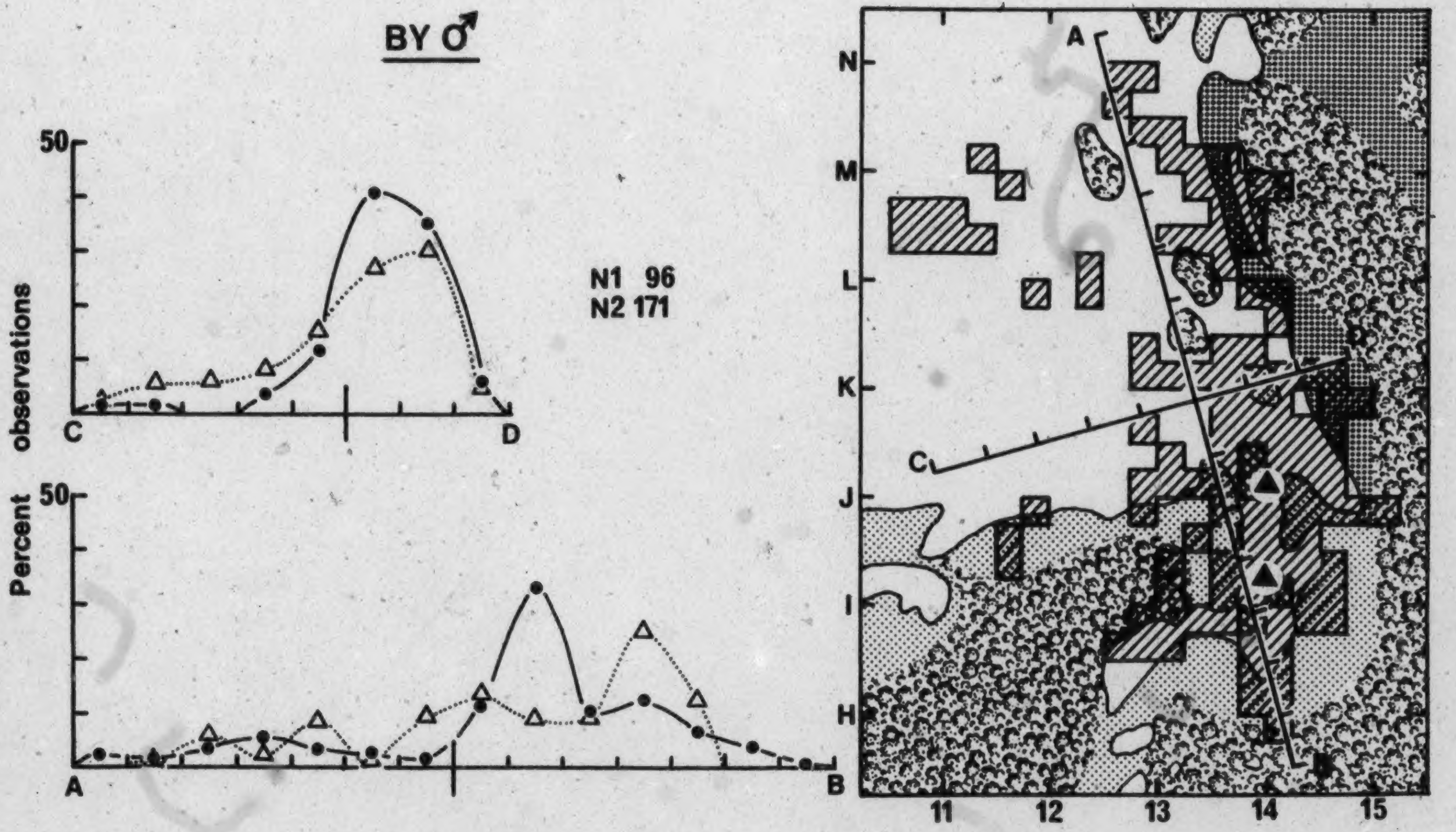
BY ♂
N1 96
N2 171
50
observations
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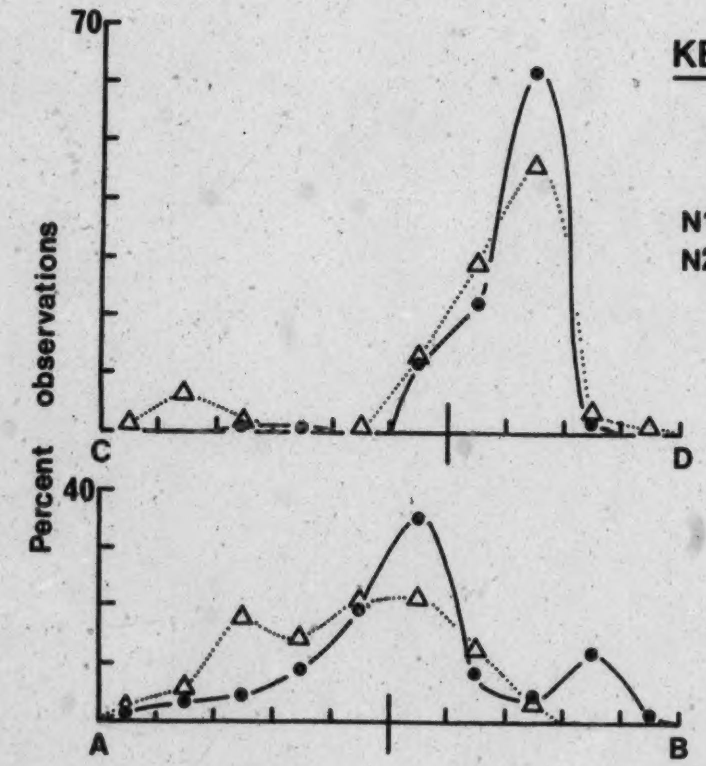
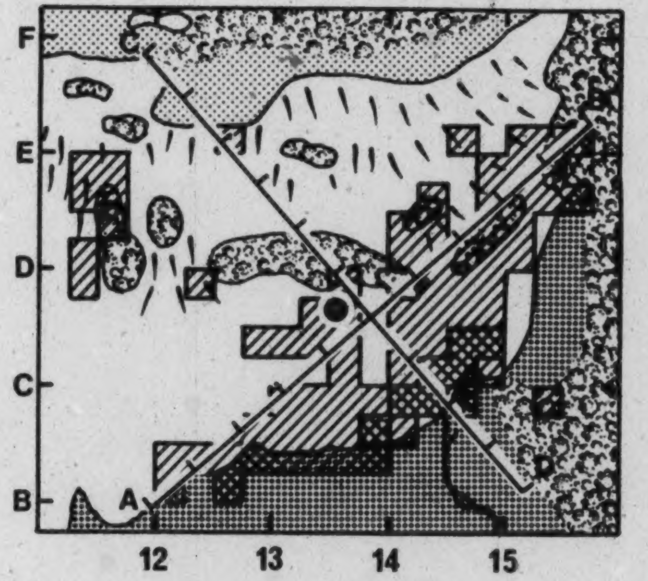


KB Q_x

N1 131
N2 126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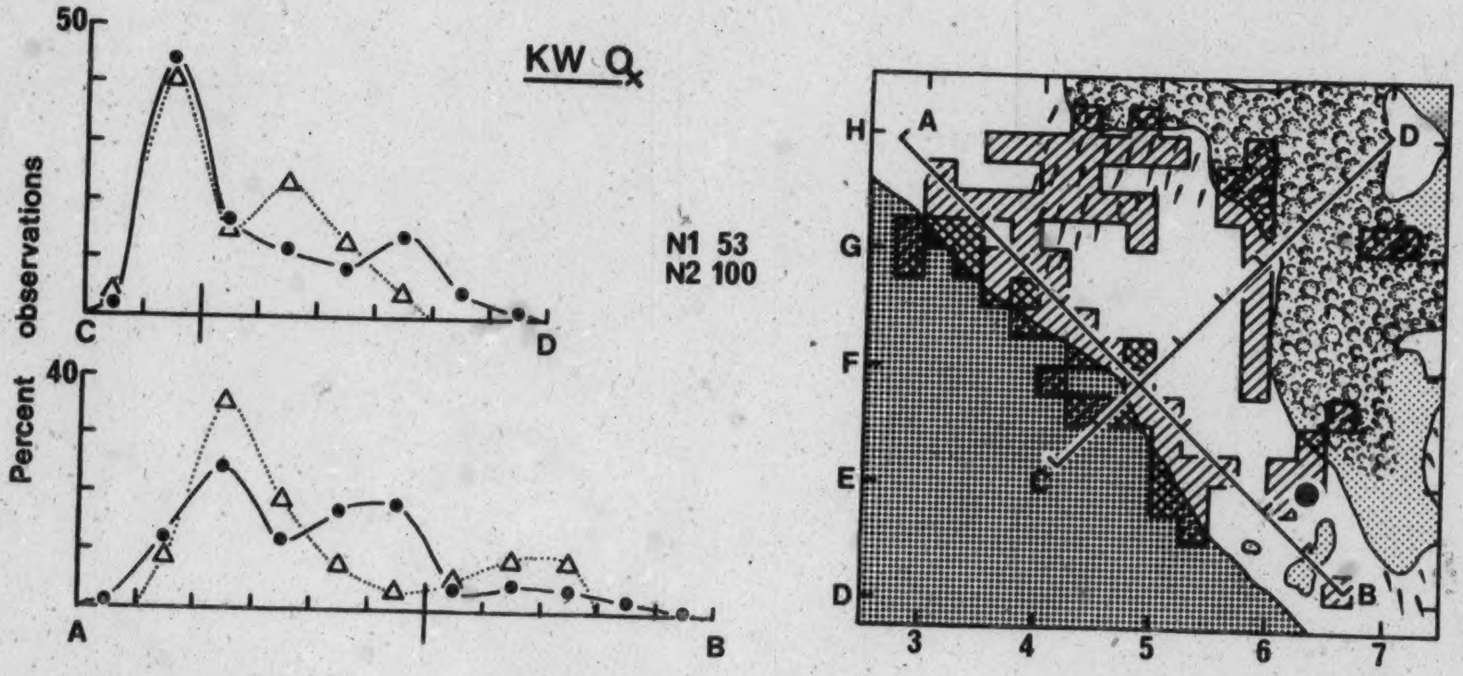
KW Q_x
N1 53
N2 100
Percent observations
50
40
C
D
A
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H
G
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E
D
3
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5
6
7
A
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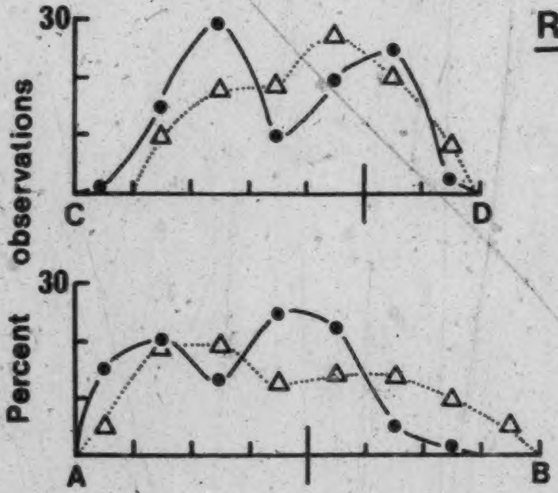
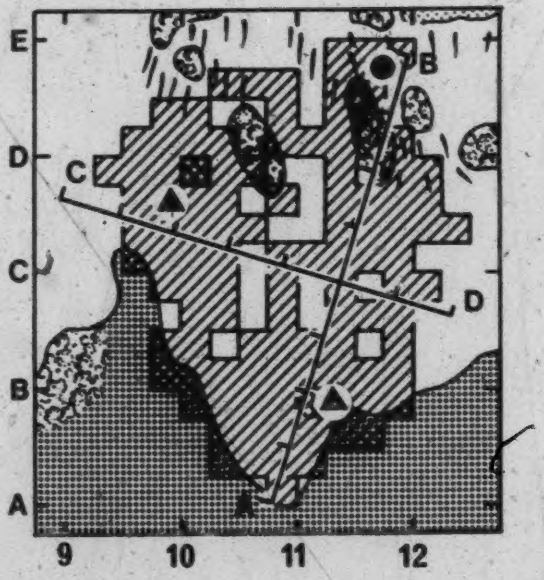
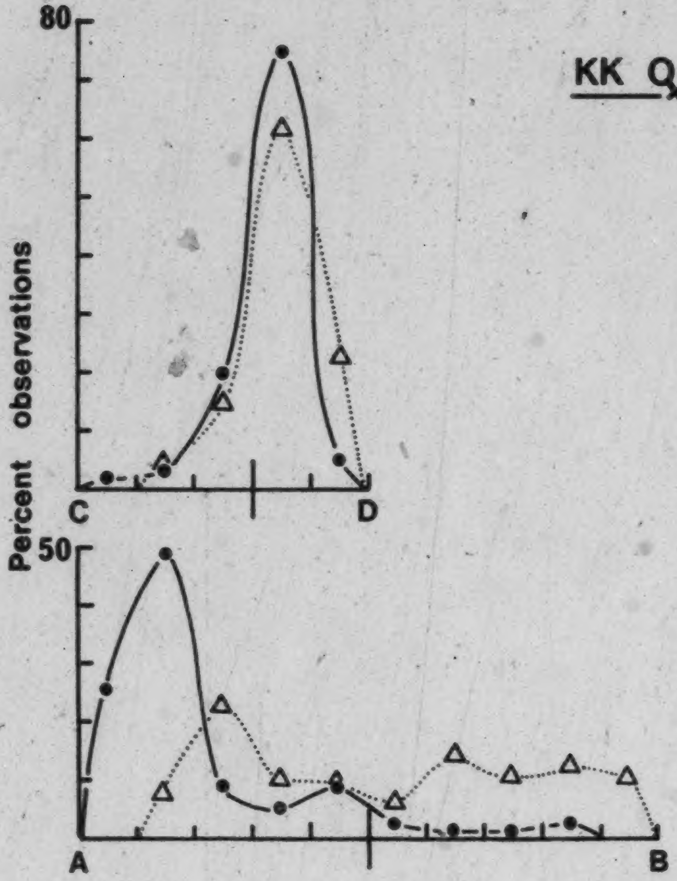


RB Q_x

N1 183
N2 195

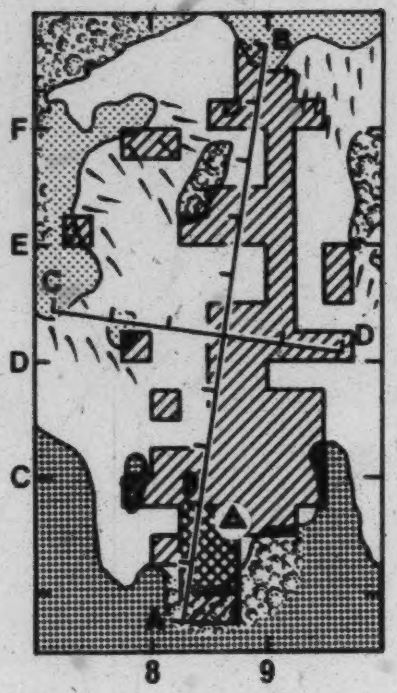


E
D
C
B
A
9
10
11
12
C
D
B



KK ♀

N1 69
N2 105


F
E
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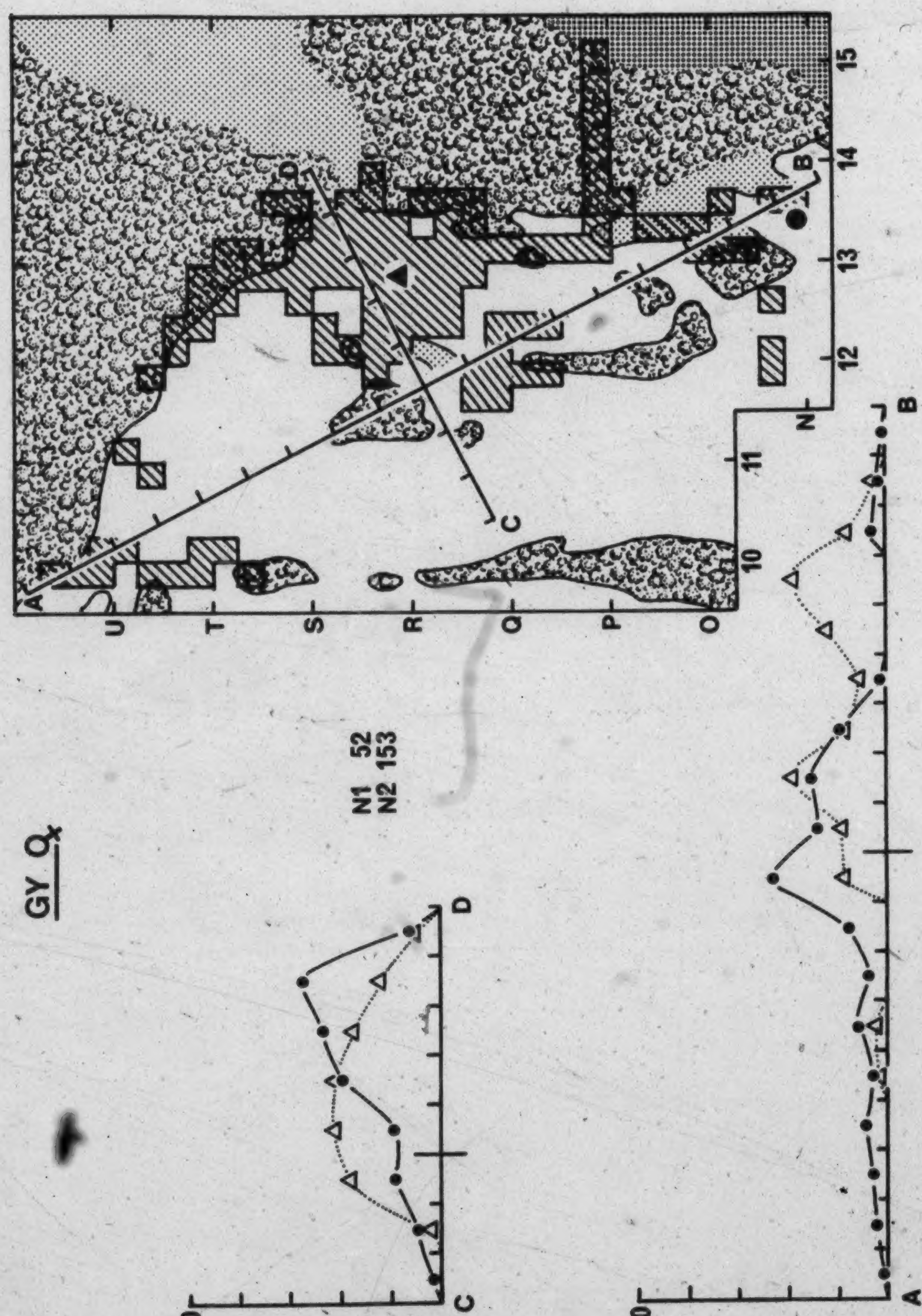
D


GY Q$_x$
N1 52
N2 153
Percent observations
50
50
C
D
A
B
U
T
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O
N
10
11
12
13
14
15

was noticed also by Sharp (1973). In males, the nest site is probably close to the haypile site since, on most days, activity appeared to start in this region. Note that, in females, a separate breeding nest was usually constructed at the periphery of the female's home range.

The distribution of observations within home ranges showed little evidence of the use of traditional runways as described for the Japanese pika (Kawamichi 1969); perhaps because runways would be unnecessary in a situation where broken talus provided an overall network of escape routes.

Among males, several aspects of home range were found to be variable, both seasonally and from area to area. These seasonal and regional differences in home range will be examined using the data from Area I in 1970, under the headings of: habitat use, intensity of use, and size. Data from 1970 were used since a large number of records was obtained for that year, and the area was studied more intensively than in other years. Data from 1969 and 1971, however, showed similar trends.

The early summer period (May - June) was the breeding season. Millar (1972) found that 100 percent of the males were fertile throughout May, 83 percent in the first half of June and 56 percent in the second half of

June; but in July very few males were fertile (9 percent and 3 percent), and none were in August. He found that two litters were produced, the first being conceived around May 9 and the second about June 12.

Haypiles were constructed in late summer (July-September). In 1969, on Area I, haypiling was not observed at all during May and only on two occasions in June, whereas it was seen 19 times in July and 15 times in August. Sharp (1973) found that adult males and females spent < 1 percent of their observed time haypiling between April and June, but in July this rose to about 20 percent for males and 5 percent for females, and in August to about 35 percent for males and 23 percent for females.

Because of these seasonal differences in behaviour, most of the temporal comparisons will be made between early summer (May - June) and late summer (July-September).

Use of Habitat within Home Range

For this analysis the study area was divided into five habitat types.

1. Talus - refers to large areas of broken rock fragments. The fragments varied in size from about 20 centimetres across to some of one or two metres.

2. Scree- refers to small loose fragments

of rock usually less than 20 centimetres in diameter. Talus was generally stable to walk on, whereas scree tended to be loose and mobile. More important, pikas could live and move amongst the talus whereas they were not able to penetrate the interstices of the rock on the scree.

3. Forest - varied from continuous stands of immature lodgepole pine with little or no ground vegetation, to small clumps of white spruce and occasional alpine fir. Ground vegetation in these areas was generally sparse, though variable, depending on the density of the trees.

4. Sparse meadows - were dry areas with bearberry (*Arctostaphylos*), juniper (*Juniperus*), and sedges (*Carex*) being dominant.

5. Lush meadows - were wet or moist areas which contained a rich abundance of grasses and herbs.

Home ranges of all adults on Area I in 1970 (except two females not observed during spring) were analysed to determine the area of each habitat within them. These areas were then expressed as percentages of the total home range, since the size of the home range was dependent on the number of times the animals had been observed. These results (Tables 1 and 2) clearly indicate a much greater proportion of rocky areas within home ranges, in

Table 1. The amount of different habitat types used by individual male pikas on Area I during summer of 1970.

	Percent of home range in each habitat					
Pika	Talus	Scree	Forest	Sparse meadow	Lush meadow	No. of observations
			Early summer			
NK	85	8	-	7	-	26
YR	64	13	3	5	15	109
NN	72	4	-	7	17	65
BY	71	2	2	16	9	96
BR	66	2	21	11	-	45
RR	77	14	2	-	7	219
GG	80	8	3	4	5	146
YW	76	3	3	2	16	43
WN	24	66	-	10	-	58
RY	80	2	10	1	7	167
GW	43	40	1	16	-	108
RG	88	4	3	-	5	251
YK	79	8	1	1	11	222
Mean	69.61	13.38	3.77	6.15	7.08	
			Late summer			
NK	43	6	17	34	-	156
YR	58	20	-	2	20	135
NN	61	5	2	9	23	128
BY	58	7	11	18	6	171
BR	73	-	20	7	-	112
RR	82	2	-	-	16	208
GG	81	5	3	-	11	226
YW	74	-	8	9	9	180
WN	20	61	7	12	-	84
RY	69	17	8	-	6	138
GW	46	30	4	19	1	94
RG	86	3	3	-	8	184
YK	62	7	3	2	26	266
Mean	62.53	12.53	6.62	8.62	9.69	

Table 2. The amount of different habitat types used by individual female pikas on Area I during summer of 1970.

	Percent of home range in each habitat					
Pika	Talus	Scree	Forest	Sparse meadow	Lush meadow	No. of observations
Early summer						
GK	58	-	4	38	-	14
GY	46	-	22	32	-	52
BB	84	-	4	12	-	32
RW	78	4	-	9	9	48
RK	81	-	2	-	17	70
KY	19	75	2	6	-	55
KK	86	9	-	4	1	69
GB	70	4	-	6	20	97
RB	75	9	5	-	11	183
KB	70	12	2	-	16	133
KW	60	21	-	-	19	53
Mean	66.09	12.18	3.73	9.73	8.45	
Late summer						
GK	90	2	4	4	-	43
GY	74	1	13	12	-	153
BB	64	-	2	34	-	76
RW	74	-	-	16	10	161
RK	80	-	11	-	9	86
KY	6	68	-	26	-	80
KK	79	5	2	-	14	105
GB	61	9	-	1	29	216
RB	85	1	2	-	12	195
KB	82	4	7	-	7	127
KW	57	12	12	1	18	100
Mean	68.36	9.27	4.82	8.55	9.00	

comparison with vegetated areas. This was consistent for nearly all animals.

To test whether or not there were any significant differences between the sexes and seasonally with respect to habitat use, a Chi-square analysis was used; first on individual animals, and secondly on the pooled data between groups -- since there were no significant differences within groups. For this analysis the habitats were lumped into two types: rocky areas (talus and scree) and vegetated areas (forest and meadow); and the number of 5 X 5 metre squares in each type compared. This was done for simplicity and because it circumvented some of the more subjective divisions, as between sparse and lush meadow areas.

Among males, only two (NK and YK) showed a significant change in the proportion of rocky to vegetated areas from early to late summer ($P < 0.01$ for NK, and $P < 0.02$ for YK). However, when the data for all males were pooled the difference was highly significant ($P < 0.001$), due to a high proportion of rocky areas used in early summer.

Analysis of the home ranges of females showed two animals with significantly different seasonal use of habitat (GK, $P < 0.05$ and GY, $P < 0.005$); both of these showed a higher proportion of rocky areas in late summer. However, when the data were pooled, females showed no statistical differences between early and late summer. Comparison between males and females revealed a significant difference ($P < 0.05$) in early summer, but no difference in late summer. These data are summarised in Fig. 4. Home ranges of males in early summer showed a significantly higher proportion of rocky areas to vegetated areas than did any of the other three categories.

This difference in habitat useage of males in the spring is probably due to an increase in the use of rocky areas rather than a decrease in use of vegetated areas, since on the average males used 37.86 squares in rocky areas and 7.06 squares in vegetated areas per 100 observations during early summer, compared to 26.17 squares in rock and 9.17 squares in vegetation in late summer.

Intensity of use within Home Range

The distribution of observations within home ranges changed seasonally, with animals spending more time at the periphery of their home ranges in early summer and more time centrally in late summer. In order to evaluate these changes, 'intensity of use' graphs were constructed for all animals which had been observed frequently enough to estimate the size of their homes ranges. (Ref. Size of Home Range).

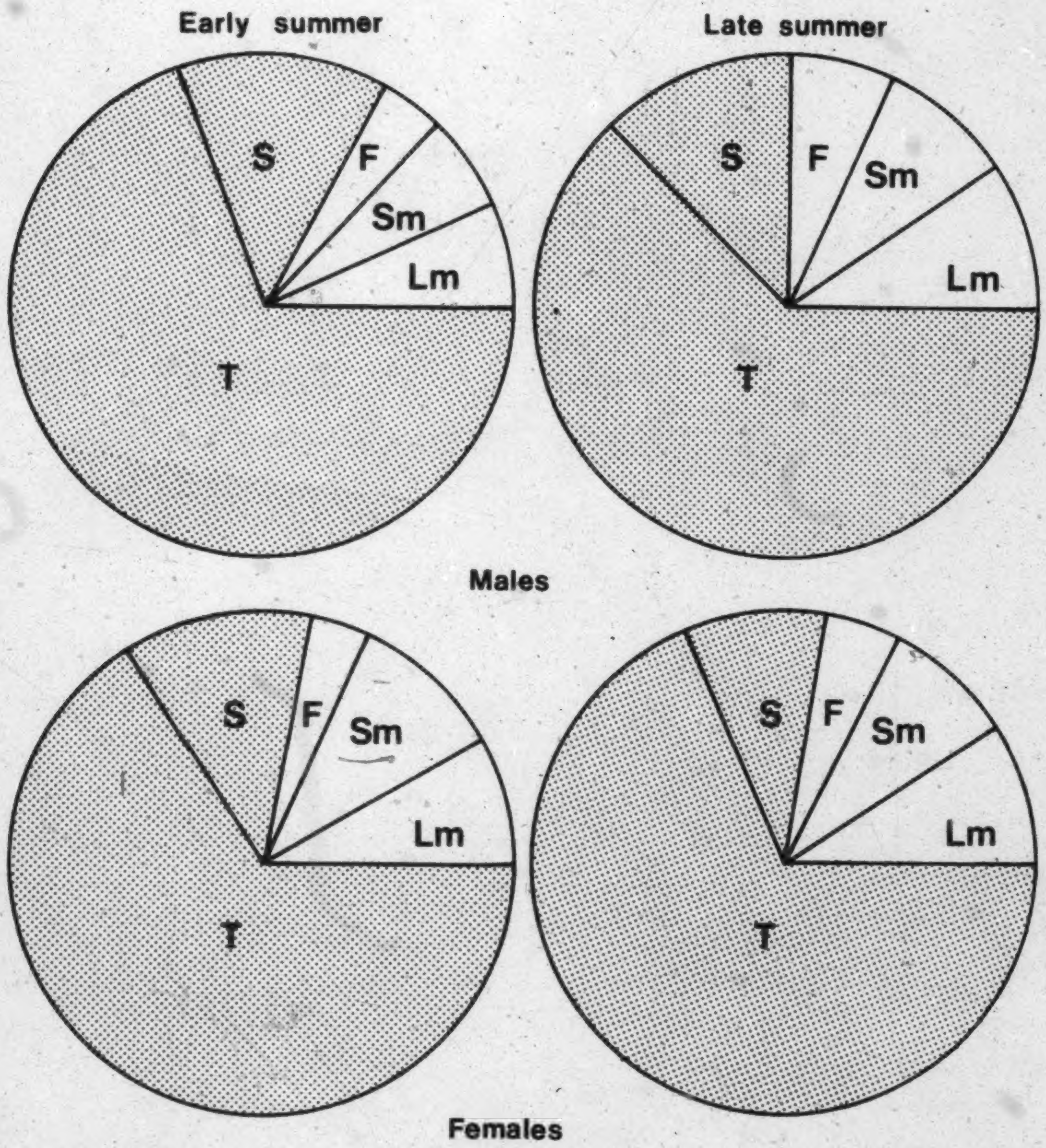


Fig. 4. A schematic representation of habitat use by male and female pikas during the early and late summer of 1970.

T = talus; S = scree; F = forest; Sm = sparse meadow; Lm = lush meadow.

A 'long axis" (AB - Fig. 3) was plotted for each home range on the line between the two most distant observation points. At right angles to this, a series of strips 10 metres wide were drawn and the number of observations occurring within each strip counted and expressed as a percentage of the total. This was also done for the 'short axis' (CD). These data, plotted seasonally, are shown in Fig. 3 for the ten animals referred to earlier. In order to make statistical comparisons, the heights of the tallest peaks on each axis were tabulated and compared seasonally with respect to sex. The results for all animals on Area I in 1970 are shown in Table 3. Using a Wilcoxon's signed-ranks test it was found that peaks were higher, indicating greater clustering of observations, in late summer than in early summer. The difference was significant for both males and females ($P < 0.01$). Males were then compared with females in the early and late summer, and no significant differences were found.

These results indicate that both males and females tend to utilize their home ranges more evenly in early summer and tend to use particular areas more intensively during late summer. This is probably caused by animals constructing haypiles in late summer producing increased activity at a haypile site. However, such things as patrolling home range boundaries in the breeding season could also account for these differences.

Table 3. Intensity of use of home ranges on Area I in 1970.

Percent of observations in highest peak along each axis

	Long axis		Short axis	
Pika	Early summer	Late summer	Early summer	Late summer
		Males		
RY	28	70	44	63
YR	28	52	38	61
RG	21	29	3[illegible]	43
GG	24	43	35	51
RR	39	45	34	55
BY	26	33	30	41
GW	66	42	41	28
YK	33	61	27	38
		Females		
KB	21	36	46	62
KK	22	48	61	74
GY	19	23	21	27
KW	36	24	41	44
RB	19	24	27	29
RW	35	33	50	54

As noted later, males have larger home ranges in early summer than in late summer. Hence this might cause the differences in intensity of use just shown. Although this must be true in part, females did not show any seasonal differences in size of home ranges, yet did show a significant difference in their use of home ranges. Thus it is likely that use intensity differences shown for males are not dependent only on differences in home range size.

Size of Home Range

With increasing amounts of data the calculated size of home ranges increases until a level is reached after which further observations do not cause a corresponding increase. The standard method for estimating home range size is, therefore, to plot size against the cumulative numbers of observations or trappings etc., and when the curve reaches an asymptote the actual home range is assumed to be represented (eg. Stickel 1954, Odum and Kuenzler 1955, Weeden 1965, Ables 1969, Stoddart 1970).

In this study, area, as measured by number of squares occupied did not produce a curve from which any reasonable estimate could be made. Instead when the dimensions of the home range (length plus breadth) were plotted with increasing observations, the curves for some animals did reach an asymptote (Figs. 5 and 6). Even in these cases a high number of observations was required for any particular time period. In order to estimate the level of the final asymptote when sufficient observations were not available, Stenger and Falls (1959) developed a method using the slope of the initial part of the curve to derive an estimate of territory size in oven birds (Seiurus aurocapillus). But the initial slopes of the curves produced from pika ranges appeared unrelated to the final asymptote, and this was probably because the observations were not sufficiently independent of each other. However, if the level at which the home range remains constant for three consecutive points on the graph is taken as an index of home range size, a constant relationship is found with the final asymptote. This index will be referred to as the 'sub-asymptote' and its relationship to the final asymptote (using animals in Figs. 5 and 6) is shown in Fig. 7.

Although the data are too few in number (and are not normally distributed) for statistical analysis they suggest that this index is very nearly the same as the final asymptote for females but is definitely lower for male pikas. This may indicate that male pikas are more likely to make exploratory excursions than females. All home range sizes used in analysis are sub-asymptotic levels.

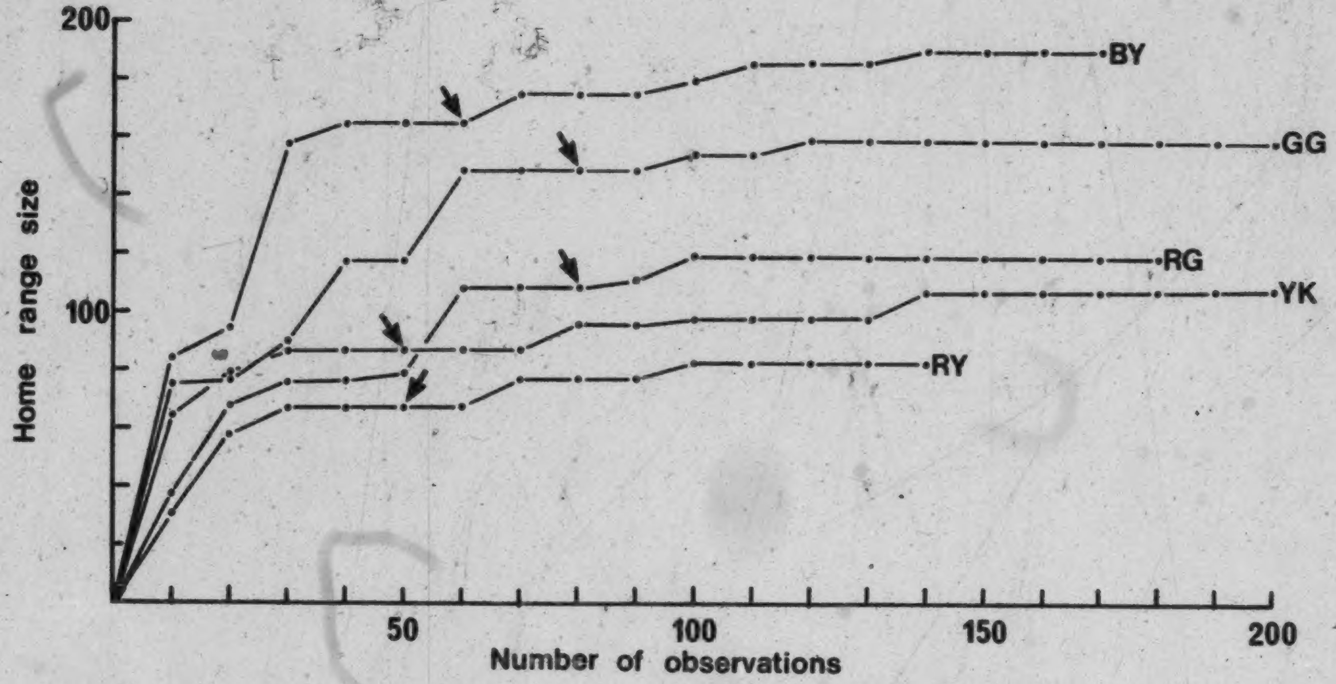


Fig. 5. Size of home range (in metres) versus number of observations for five males during late summer 1970. Animals were selected on the basis that the curves for home range size appeared to reach an asymptote. Arrows indicate sub-asymptote.

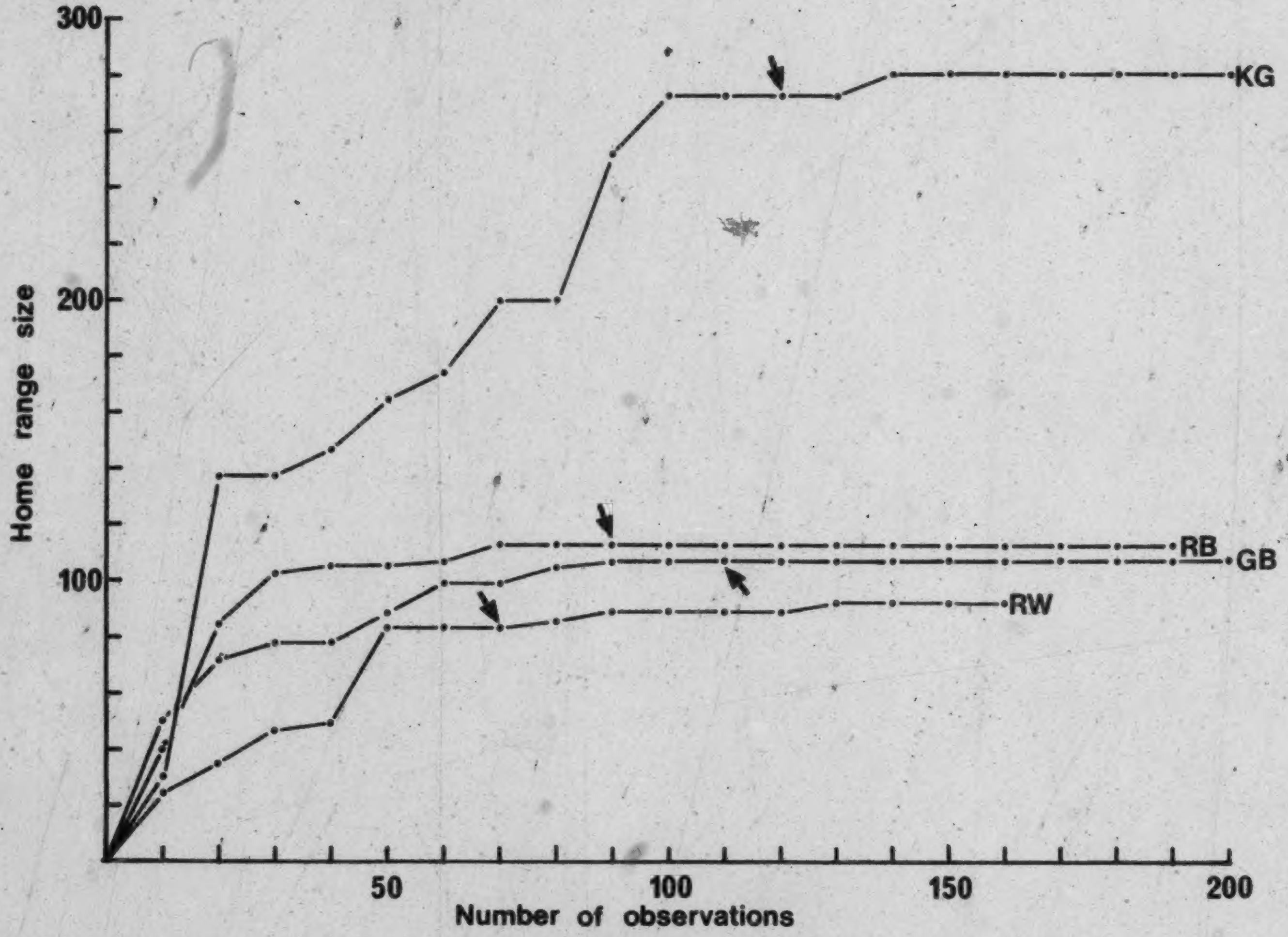


Fig. 6. Size of home range (in metres) versus number of observations for four females during late summer 1970. Animals were selected on the basis that the curves for home range size appeared to reach an asymptote. Arrows indicate sub-asymptote.

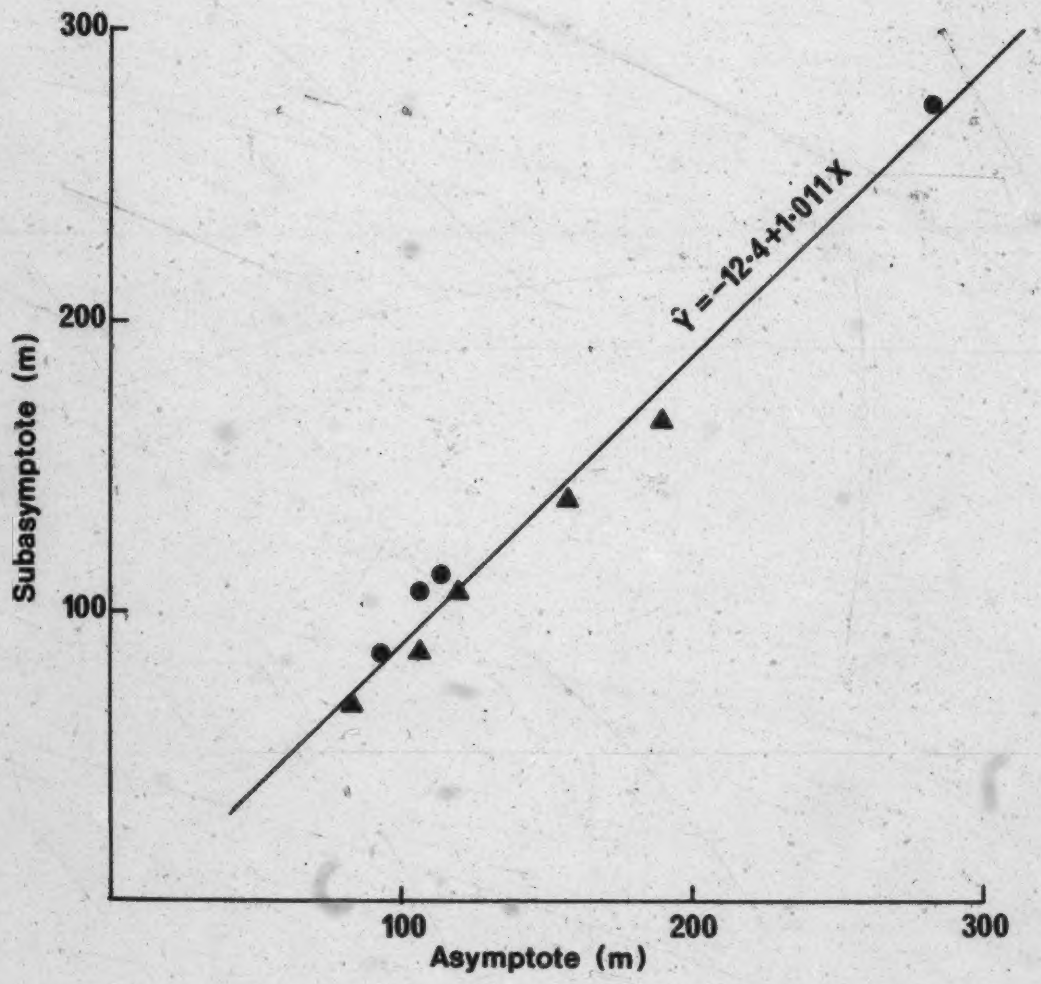


Fig. 7. Relationship between sub-asymptotes and asymptotes of home ranges of five males and four females shown in Figs. 5 and 6.

▲ Males.
● Females.

Seasonal Variation

Sizes of home ranges of all adults on Area I in 1970 are shown in Table 4. In this table, figures in brackets are home range sizes below the sub-asymptote; they are included only for comparative inspection and were not used in statistical calculations. Where sufficient data are available, an estimate for each month is given -- otherwise months are combined as early or late summer. Where estimates are made for both months in one season the final figure is given by the average of the two months. Seasonal changes in home range size were examined using a Wilcoxon signed-ranks test. This meant that only animals for which there were figures for both seasons were included in the analysis.

In males, home ranges were significantly larger in early than in late summer ($P < 0.025$). This decrease in size with the progression of summer appears to be a gradual shrinkage rather than a rapid switch since the August-September figures are also significantly lower than those in July ($P < 0.05$). Unfortunately sample sizes were too small to make comparisons between May and June, and June and July.

This change in size of home range correlates with the change in use of habitat described earlier, which suggests that expansion of home ranges in early summer is

Table 4. Home range sizes of all adult pikas on Area I during the summer of 1970. Ranges are measured in metres (length + breadth) and are 'sub-asymptotes.'

Pika	May	June	Early Summer	July	Aug-Sept	Late Summer
			Males			
YR	-	-	145	-	-	140
BY	-	-	192	-	-	164
RG	116	149	132	108	96	102
RR	-	-	110	98	84	91
RY	155	87	121	67	-	67
YK	-	-	165	87	81	84
GG	122	-	122	149	124	136
GW	-	-	132	-	-	124
NK	-	-	(>181)	151	-	151
NN	-	-	(>123)	-	-	109
WN	-	-	(>110)	-	-	116
YW	-	-	(>236)	251	245	248
			Females			
BB	-	-	(>189)	-	-	150
GB	-	-	(>136)	107	71	89
GK	-	-	(>83)	-	-	(>125)
GY	-	205	205	-	-	219
KB	-	-	139	-	-	151
KG	-	-	-	-	-	273
KK	-	-	111	-	-	134
KW	-	-	112	-	-	154
KY	-	-	-	-	-	93
RB	-	-	129	-	-	112
RK	-	-	-	-	-	-
RW	-	-	89	83	74	78
WB	-	-	-	-	-	(>191)

accomplished by the inclusion of larger areas of talus.

In females there was no significant change in the home range size from season to season. Although the sample sizes are small, it is clear that there are no seasonal trends.

Sizes of home ranges were compared between males and females during both seasons using paired and non-paired non-parametric statistical tests. No significant differences were found although males appeared to have generally larger home ranges than females in early summer when adjacent males and females were considered. It is probable that the wide variation in home range sizes and the small sample sizes account for this lack of significance.

Regional Variation

Apart from the seasonal variation in size of home ranges and a general variability between individuals there appeared to be marked regional differences in home range size within and between study areas. This was apparent on Area I where animals on the upper section of the slide (above grid line 'H') had large home ranges while those on the lower section (below grid line 'H') had smaller ranges (Table 5). This difference was significant among males ($P = 0.005$ - Mann Whitney U test), but not among

Table 5. Comparison of home range sizes from upper and lower sections of Area I.

Sub-asymptotes - measured in metres			
Lower section		Upper section	
Males	Females	Males	Females
116	89	248	150
109	151	151	219
124	134	164	273
136	154		
84	93		
67	112		
91	78		
102			
140			

females; probably due to small sample size.

Associated with this were two other variables which could be important in explaining the difference. (1) The density of individuals was lower on the upper section of talus. (2) The amount of food available, as indicated by the standing crop of herbaceous vegetation, seemed to be much lower on the upper section of talus. These aspects were examined in more detail.

Centres of activity were calculated for all adult animals on Area I during late summer 1970, using the method described by Hayne (1949). The distance from the centre of activity of one animal to the centre of activity of its nearest neighbour of the same sex was taken as an index of relative density. These indices for all adults on Area I are shown in Table 6. Indices for males on the upper section of talus were significantly higher than those on the lower section ($P < 0.005$ - Mann Whitney U test). This was also true for females ($P < 0.001$).

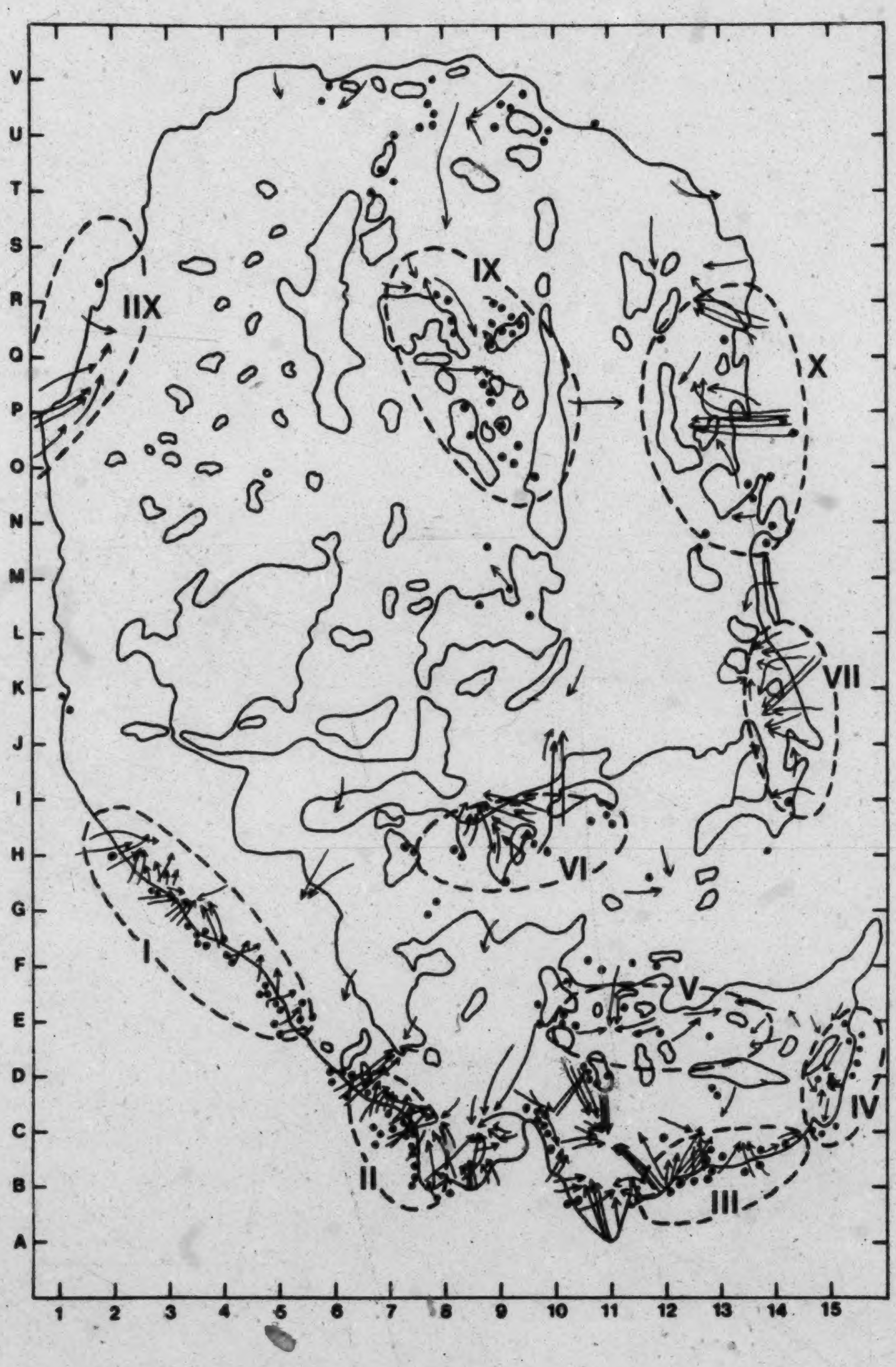
In order to evaluate the relative amounts of food available in different areas, all observations of feeding and haying behaviour made during July - September 1970 were plotted on a map of Area I (Fig. 8). From these observations, ten feeding areas were chosen; five from the upper section of slide and five from the lower (Fig. 8). Feeding areas were sampled by clipping all ground vegeta-

Table 6. Comparison of densities from upper and lower sections of Area I.

Distance to nearest neighbour (metres) of same sex

Lower section		Upper section	
Males	Females	Males	Females
32	14	105	93
32	14	105	93
42	35	188	85
45	44	128	85
45	20		92
14	20		
14	52		
56	52		
68			

Fig. 8. Observations of feeding and haying behaviour on Area I from July to September 1970. Closed circles - observations of pikas feeding; arrows - movements of pikas carrying vegetation; I - V feeding areas on lower section of slide; VI - X feeding areas on upper section of slide.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tion (excluding mosses and lichens) from five 1/10 square metre plots on each feeding area. However, one species, juniper (Juniperus), was excluded since it was extremely widespread and abundant but was almost never used by pikas (Millar 1971). Because of the nature of the terrain (often only clumps of vegetation between broken rocks), plots were subjectively chosen within these feeding areas so that only the densest patches of vegetation were sampled. Hence the weights are maxima rather than random samples. These results are shown in Table 7. The mean weights from the upper section of the slide were significantly smaller than from the lower section ($P < 0.001$ - t test).

These results have to be viewed with caution since they do not show any cause and effect relationship. However, they suggest two principles which could be important in the dispersion of pikas. (1) Size of home range appears related to density, suggesting the use of space tends to be exclusive between individuals of the same sex. (2) Size of home range and, therefore density, appears related to the relative abundance of an accessible source of food.

Table 7. Comparison of weights of vegetation from upper and lower sections of Area I.

Feeding area	Dry wgt. (grams) of vegetation on 1/10 sq. metre plot					Mean
			Lower section			
I	34.5	33.8	32.2	53.1	37.0	38.12
II	29.1	34.5	40.3	57.0	23.5	36.88
III	35.5	35.8	40.1	36.3	29.1	35.36
IV	8.0	27.8	14.1	32.6	28.5	22.20
V	10.6	1.5	74.1	82.9	7.0	35.22
			Upper section			
VI	6.8	9.1	14.2	10.0	8.3	9.68
VII	13.2	9.4	14.0	13.9	8.9	11.88
VIII	5.2	15.2	9.3	5.0	4.3	7.80
IX	5.3	12.3	6.5	3.4	5.3	6.56
X	13.8	23.0	24.1	9.5	4.9	15.06

SPATIAL ORGANISATION OF ADULTS

This section deals with dispersion of adult pikas and with the social factors which appear to give rise to it; the movement and settlement of juveniles being considered later.

Although the spatial organisation should be considered as an interrelated system with variations in one aspect causing compensatory changes in other aspects, it is dealt with here in three separate subsections: (1) male - female spacing, (2) male - male spacing, (3) female - female spacing. Only data from Area I during 1970 and 1971 are used in this analysis.

Male - Female Spacing

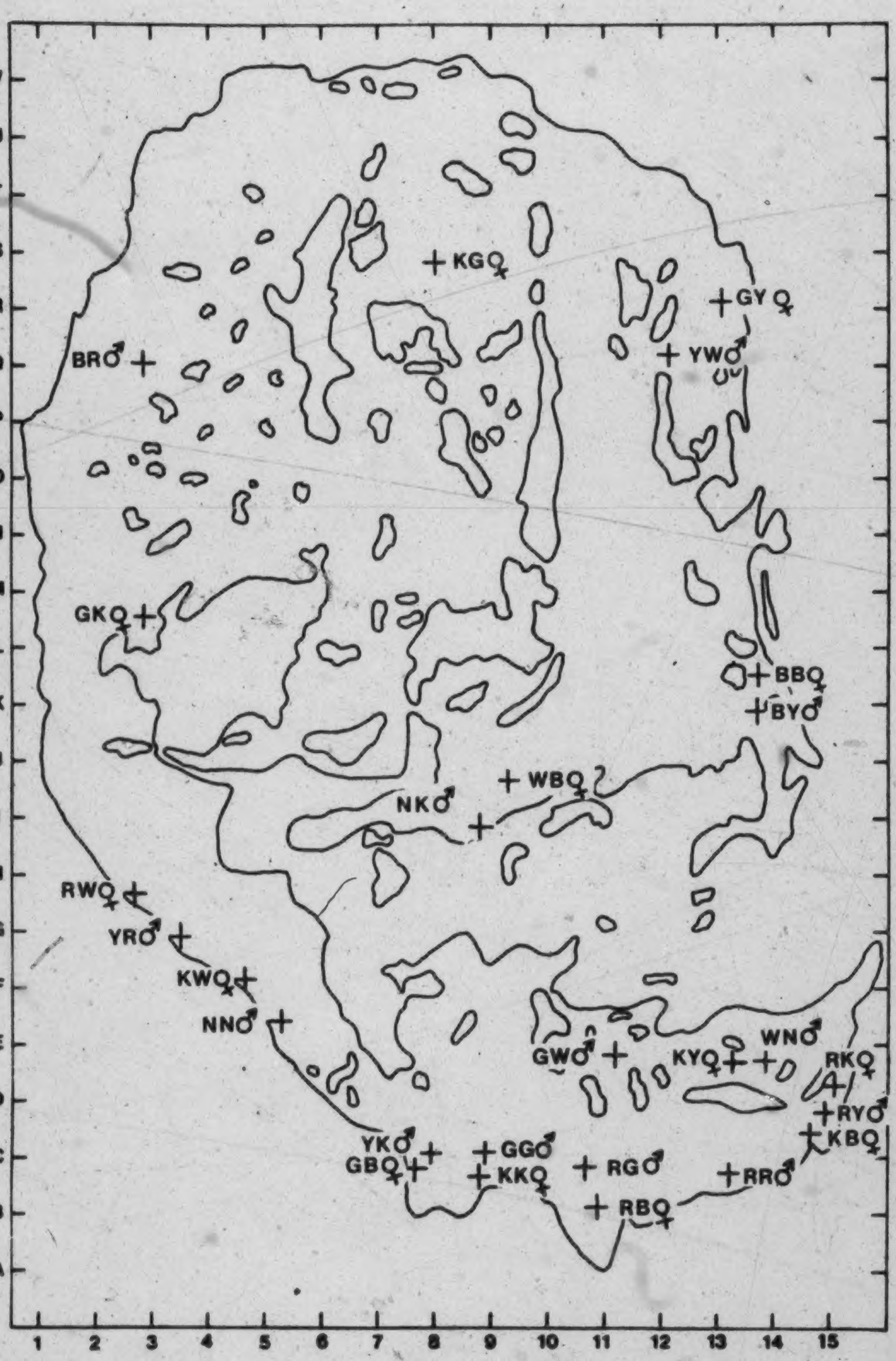
At birth the sex ratio in pikas was found by Millar (1971) to be almost 1:1. On Area I the sex ratio of adults is shown in Table 8. While none of these figures differed significantly from a 1:1 sex ratio (using Chi-square analysis), there was a slight bias in favour of males, especially during 1971.

When centres of activity of adults were plotted (Fig. 9), there appeared to be a close association between

Table 8. Number of adults by sex on Area I, 1969 - 1972

		Males	Females
1969	Early summer	12	11
	Late summer	10	10
1970	Early summer	14	14
	Late summer	14	13
1971	Early summer	19	13
	Late summer	17	10
1972	Early summer	13	9

Fig. 9. Calculated centres of activity for adult pikas on Area I, July - September 1970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RB♀

males and females. With few exceptions adults seemed to occur in pairs. When home ranges were plotted for individual pairs this association was even more striking. An example is shown in Fig. 10, where the female's home range varied little seasonally. During the late summer both animals appeared to have almost exactly the same outer limits to their home ranges, however there were areas used exclusively by each.

Another pair is shown in Fig. 11 where the home ranges were almost entirely separate, perhaps indicating little association unless one refers back to Fig. 9 and considers the centers of activity relative to the other members of the population. This separation was more noticeable at low than at high densities.

These same principles are illustrated in Fig. 12 but with a slight variation. Here two pairs of animals (BY:BB, and GY:YW) showed a clear boundary between pairs, especially along the edge of the rock slide, and yet in both pairs, the males and females used different areas most intensively. This situation was further complicated by a third female (KG) which seemed to be unpaired, although YW extended his home range right across hers. In this situation there was still a clear boundary between the two adjacent females, indicating that females may maintain their own boundaries irrespective of males. In

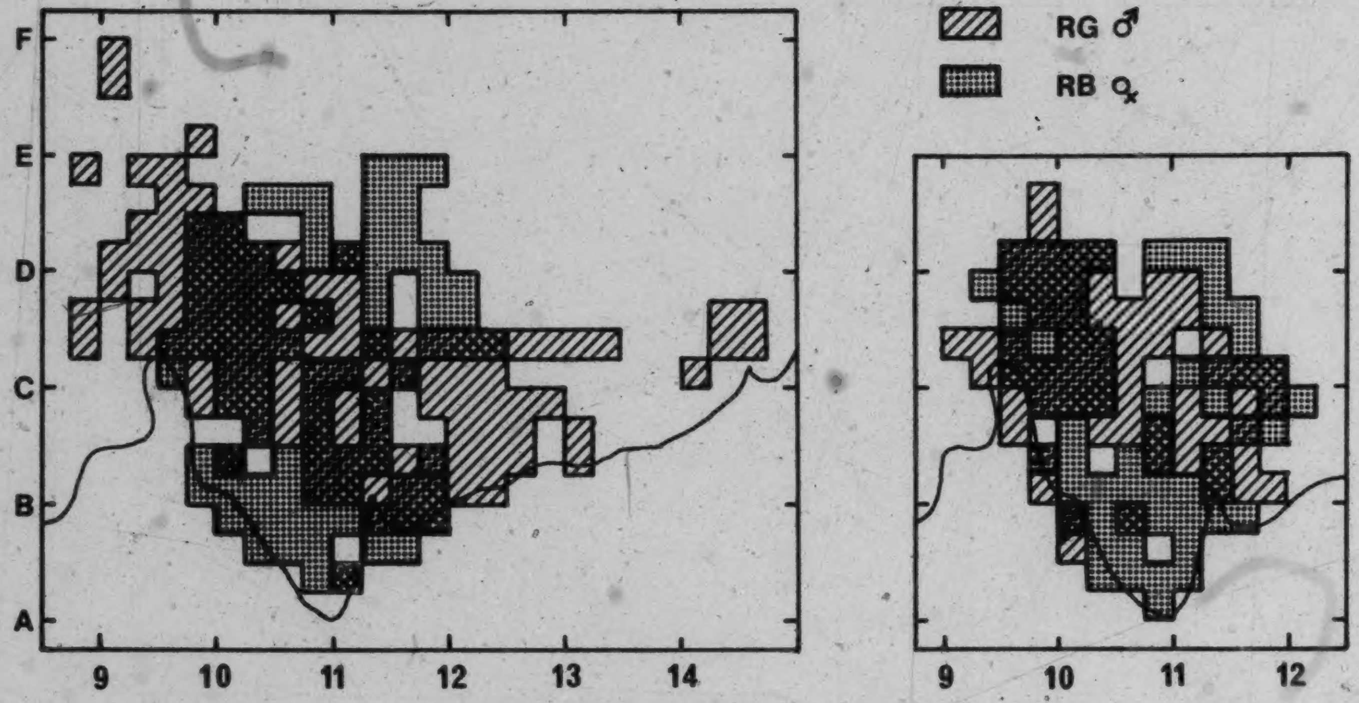

F
E
D
C
B
A
9
10
11
12
13
14
RG ♂
RB ♀
9
10
11
12

Fig. 10. Home ranges of a pair of pikas during early summer (left) and late summer (right) on Area I in 1970. Number of observations: Early summer, RG = 255, RB = 183. Late summer, RG = 184, RB = 197

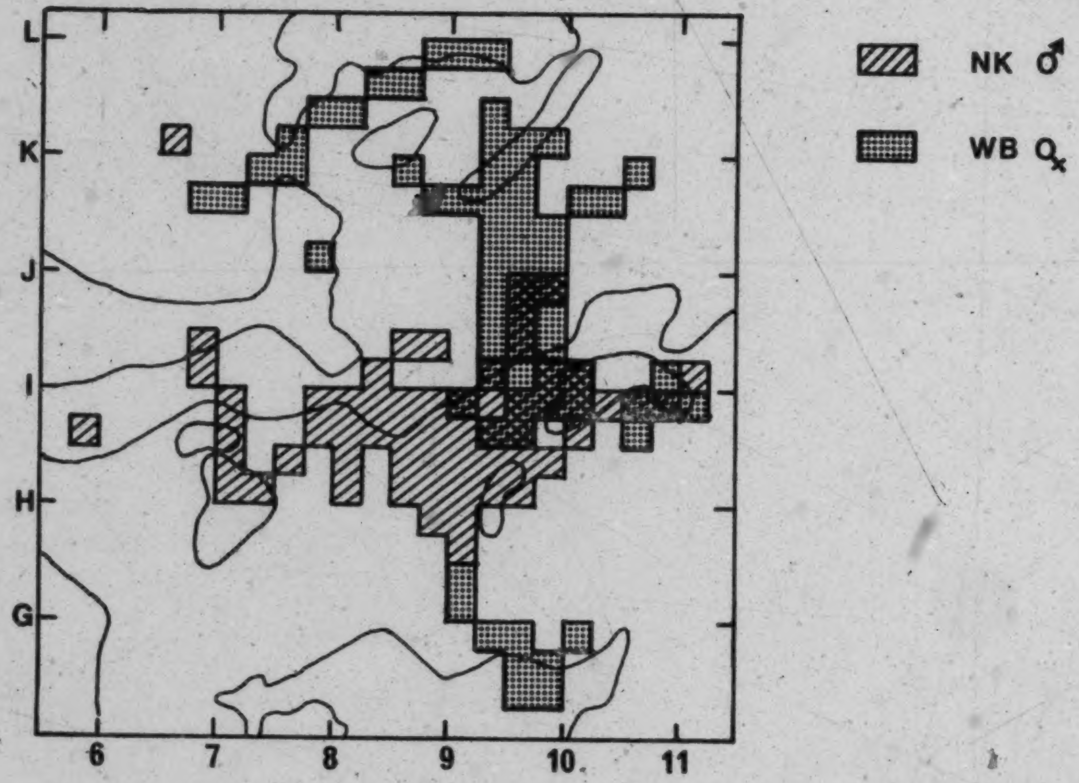
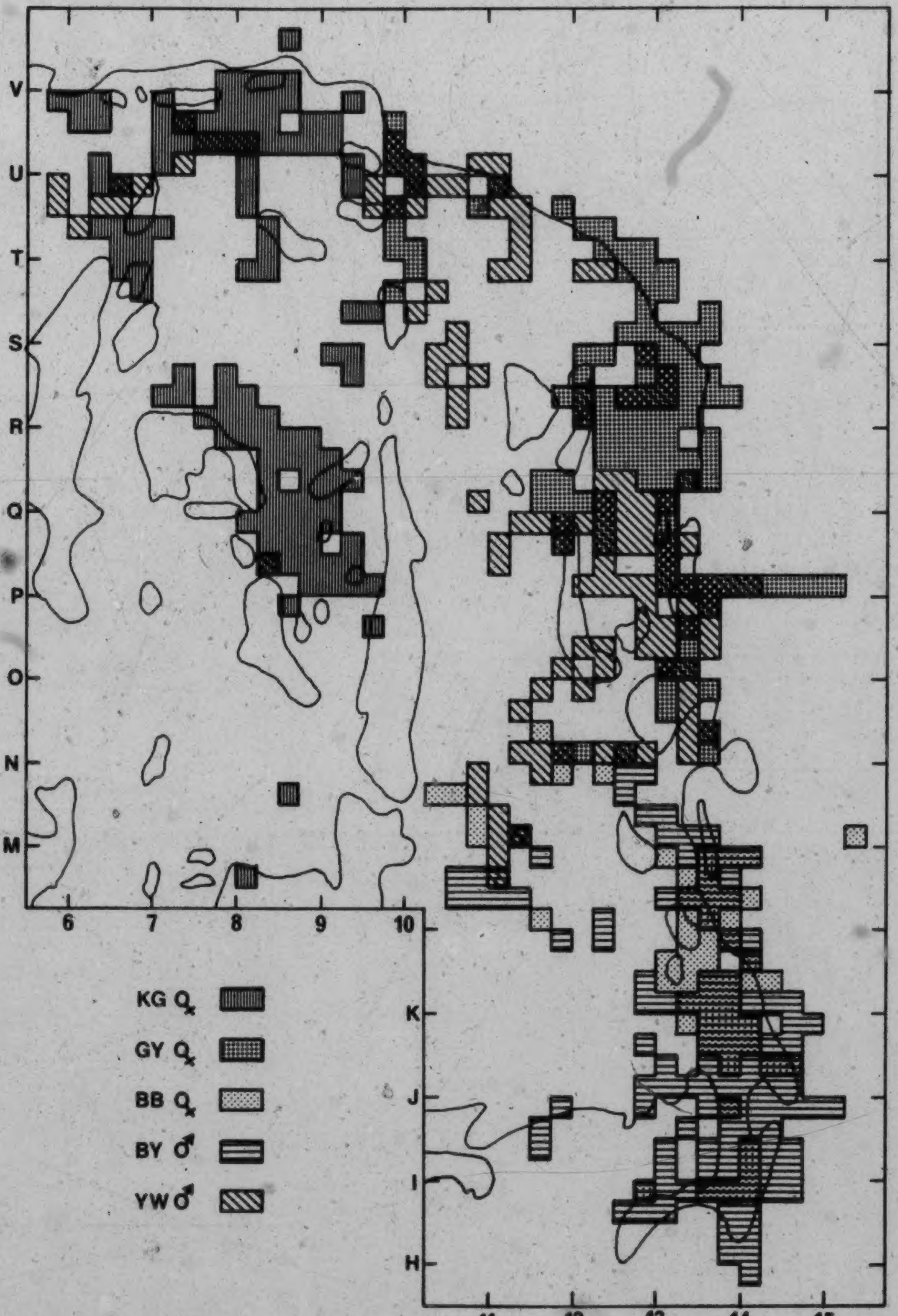

L
K
J
I
H
G
6
7
8
9
10
11
NK ♂
WB ♀

Fig. 11. Home ranges of a pair of pikas during late summer on Area I in 1970, number of observations: NK = 156, WB = 89.

Fig. 12. Home ranges of five pikas during summer on Area I in 1970.

Number of observations: BY = 267, YW = 223, BB = 108, GY = 206, KG = 202.


V
U
T
S
R
Q
P
O
N
M
K
J
I
H
6
7
8
9
10
11
12
13
14
15
KG ♀
GY ♀
BB ♀
BY ♂
YW ♂

general, however, paired animals seemed to have similar outer limits to their ranges. This particular situation could be explained in two ways: (1) that there was originally another pair present, the male of which died leaving female KG, and YW's range extension merely exploited this vacancy; (2) that YW in fact had an exceptionally large home range which was of sufficient size to include two females. This latter explanation appeared to be more likely since the situation remained largely unaltered in three years, except KG replaced a female lost in 1969 (trap mortality), and a male was present near KG in the spring of 1971 but failed to survive the summer.

Since there was much variation in spatial relationships among adults it is difficult to extrapolate general principles from selected examples. Therefore, the whole adult population on Area I for 1970 and 1971 was analysed with respect to overlap between home ranges of males and females.

These results are shown in Tables 9 and 10. Overlap is expressed as a percentage of a female's home range overlapped by all other males, and this is based on the total number of 5 X 5 metre squares in a female's home range and the number shared with each male. Clearly no home range of one male can overlap a female's home range more than 100 percent, but including all males, a female's

Table 9. Matrix showing relative amounts of home range overlap between individual males and females on Area I 1970.

Male	Percent of female's home range overlapped by male												
	Early summer												
	RK	KB	KY	RB	KK	GB	KW	RW	GK	KG	GY	BB	WB
RY	86	47	4	3	-	-	-	-	-	-	-	-	-
RR	24	33	27	6	-	-	-	-	-	-	-	-	-
WN	-	-	42	3	-	-	-	-	-	-	-	-	-
GW	-	11	23	10	4	-	-	-	-	-	-	-	-
RG	21	25	-	55	16	2	-	-	-	-	-	-	-
GG	-	-	-	-	71	32	-	-	-	-	-	-	-
YK	-	-	-	7	44	68	6	-	-	-	-	-	-
NN	-	-	-	-	-	-	19	-	-	-	-	-	-
YR	-	-	-	-	-	-	25	38	-	-	-	-	-
BR	-	-	-	-	-	-	-	-	25	-	-	-	-
YW	-	-	-	-	-	-	-	-	-	-	10	4	-
BY	-	-	-	-	-	-	-	-	-	-	-	48	-
RN	-	-	-	-	-	-	-	-	-	-	-	-	-*
NK	-	-	-	-	-	-	-	-	-	-	-	-	-
Total squares occupied by female	29	57	26	87	45	50	36	24	12	*	41	25	*
	Late summer												
	RK	KB	KY	RB	KK	GB	KW	RW	GK	KG	GY	BB	WB
RY	62	44	3	-	-	-	-	-	-	-	-	-	-
RR	14	35	3	3	-	-	-	-	-	-	-	-	-
WN	10	9	55	-	-	-	-	-	-	-	-	-	-
GW	-	-	9	13	-	-	-	-	-	-	-	-	-
RG	-	2	-	51	-	-	-	-	-	-	-	-	-
GG	-	-	-	-	71	27	-	-	-	-	-	-	-
YK	-	-	-	-	39	69	2	-	-	-	-	-	-
NN	-	-	-	-	-	12	19	-	-	-	-	-	-
YR	-	-	-	-	-	-	31	24	-	-	-	-	-
BR	-	-	-	-	-	-	-	-	7	-	-	-	-
YW	-	-	-	-	-	-	-	-	-	5	12	-	-
BY	-	-	-	-	-	-	-	-	-	-	1	43	-
RN	-	-	-	-	-	-	-	-	-	-	-	-	-?
NK	-	-	-	-	-	-	-	-	-	-	-	-	23
Total squares occupied by female	29	45	34	67	31	65	54	38	27	108	84	42	66

* Insufficient data.   ? animal disappeared from population

Table 10. Matrix showing relative amounts of home range overlap between individual males and females on Area I, 1971

Males	Percent of female's home range overlapped by males												
	Early summer												
	RK	KB	KY	RB	KW	RW	N̄N	KG	GY	NG	BB	ȲY	WB
YB1	63	30	-	-	-	-	-	-	-	-	-	-	-
RY	95	33	-	4	-	-	-	-	-	-	-	-	-
RR	21	79	-	4	-	-	-	-	-	-	-	-	-
WN	-	-	52	-	-	-	-	-	-	-	-	-	-
GW	-	3	15	13	4	-	-	-	-	-	-	-	-
RG	-	3	4	65	-	-	-	-	-	-	-	-	-
BW1	-	15	4	46	-	-	-	-	-	-	-	-	-
GG	-	-	-	1	-	-	-	-	-	-	-	-	-
YK	-	-	-	-	42	12	-	-	-	-	-	-	-
ȲB	-	-	-	-	2	-	-	-	-	-	-	-	-
ȲR	-	3	-	13	19	44	-	-	-	-	-	-	-
BR	-	-	-	-	-	9	5	-	-	-	-	-	-
WK	-	-	-	-	-	-	-	-	13	-	-	-	-
YW	-	-	-	-	-	-	-	12	13	11	-	-	4
BY	-	-	-	-	-	-	-	-	-	-	65	17	-
WY	-	-	-	-	-	-	-	-	-	-	8	26	4
NK	-	-	-	-	-	-	-	-	-	-	-	-	22
YN	-	-	-	-	-	-	-	-	-	-	-	-	-
WW1	-	-	-	-	2	-	-	-	-	-	-	-	-
Total squares occupied by female													
	19	33	27	78	52	34	19	25	47	9	26	30	23

(continued)

Table 10, continued

Males	Percent of female's home range overlapped by males												
	Late summer												
	RK	KB	KY	RB	KW	RW	N̄N	KG	GY	NG	BB	ȲY	WB
YB1	-	-	-	-	-	-	-	-	-	-	-	-	-
RY	-	-	-	-	-	-	-	-	-	-	-	-	-
RR	-	-	10	-	-	-	-	-	-	-	-	-	-
WN	-	-	21	-	-	-	-	-	-	-	-	-	-
GW	-	-	-	-	-	-	-	-	-	-	-	-	-
RG	-	-	-	33	-	-	-	-	-	-	-	-	-
BW1	-	-	3	36	-	-	-	-	-	-	-	-	-
GG	-	-	-	6	-	-	-	-	-	-	-	-	-
YK	-	-	-	-	-	-	-	-	-	-	-	-	-
ȲB	-	-	-	-	-	-	-	-	-	-	-	-	-?
ȲR	-	-	-	-	38	24	-	-	-	-	-	-	-
BR	-	-	-	-	-	-	10	-	-	-	-	-	-
WK	-	-	-	-	-	-	-	-	-	-	-	-	-?
YW	-	-	-	-	-	-	-	-	5	-	-	-	-
BY	-	-	-	-	-	-	-	-	-	-	28	6	-
WY	-	-	-	-	-	-	-	-	-	-	-	9	-
NK	-	-	-	-	-	-	-	-	-	-	-	-	6
YN	-	-	-	-	-	-	-	-	-	-	-	-	3
WW1	-	-	-	-	-	-	-	-	-	-	-	-	-
Total squares occupied by female													
	?	?	29	33	34	33	39	17	20	?	18	35	32

[?] Animal disappeared from population

home range may be overlapped by a factor greater than 100 percent.

These figures, besides showing general trends, also point out interesting details and variations among individual animals. For example, in 1970, RG by expansion of his home range in early summer was able to overlap the ranges of three other females besides his 'mate' (RB); by late summer however he only overlapped one other. Conversely GW appeared to be an unpaired male since, although his home range did overlap other females, none of them were strongly associated with him. In 1971 the proportion of males was much higher relative to the females and more of these males appeared to be unpaired -- examples were WW1, YN, YB1, and GW. Others were left single because of the death of the female they were paired with previously. GG illustrated this situation in 1971 as did YK, except that the latter managed to temporarily pair with a neighbouring female (KW) who had lost her mate.

An examination of these data shows three major trends in the use of space between males and females.

1. There is a much greater degree of overlap between males and females in early compared with late summer. This can be clearly seen in the tables. Using a Wilcoxon's signed ranks test, the percentage of overlap was found to be statistically greater in early summer;

$P = 0.001$ for 1970, and $P < 0.005$ for 1971. This is in part a reflection of larger sizes of home ranges in males early in the season.

2. If the above relationship is examined using paired males and females only, there is also a significant decrease in the amount of space shared in late summer when compared with early summer; animals which could not be associated with one male or female were not used in the calculations. Using a Wilcoxon's signed ranks test the overlap was significantly greater in the early summer compared with the late summer ($P < 0.05$ for 1970 and $P < 0.005$ for 1971).

3. In Tables 9 and 10, animals are plotted in an order of approximately decreasing density (ie. from the bottom of the slide to the top); density decreasing from left to right for females and top to bottom for males. It then becomes clear that with increasing density the amount of overlap by males increases also. This situation might be expected where neighbouring males contribute to a lot of the overlap but not necessarily when members of pairs only are considered. To examine this statistically an index of relative density was correlated with the amount of overlap. This index was the distance from one female to the nearest female neighbour, against which was correlated (a) the percentage overlap by all males, and (b) by the paired male only. The results are shown graphically in Fig. 13. Only

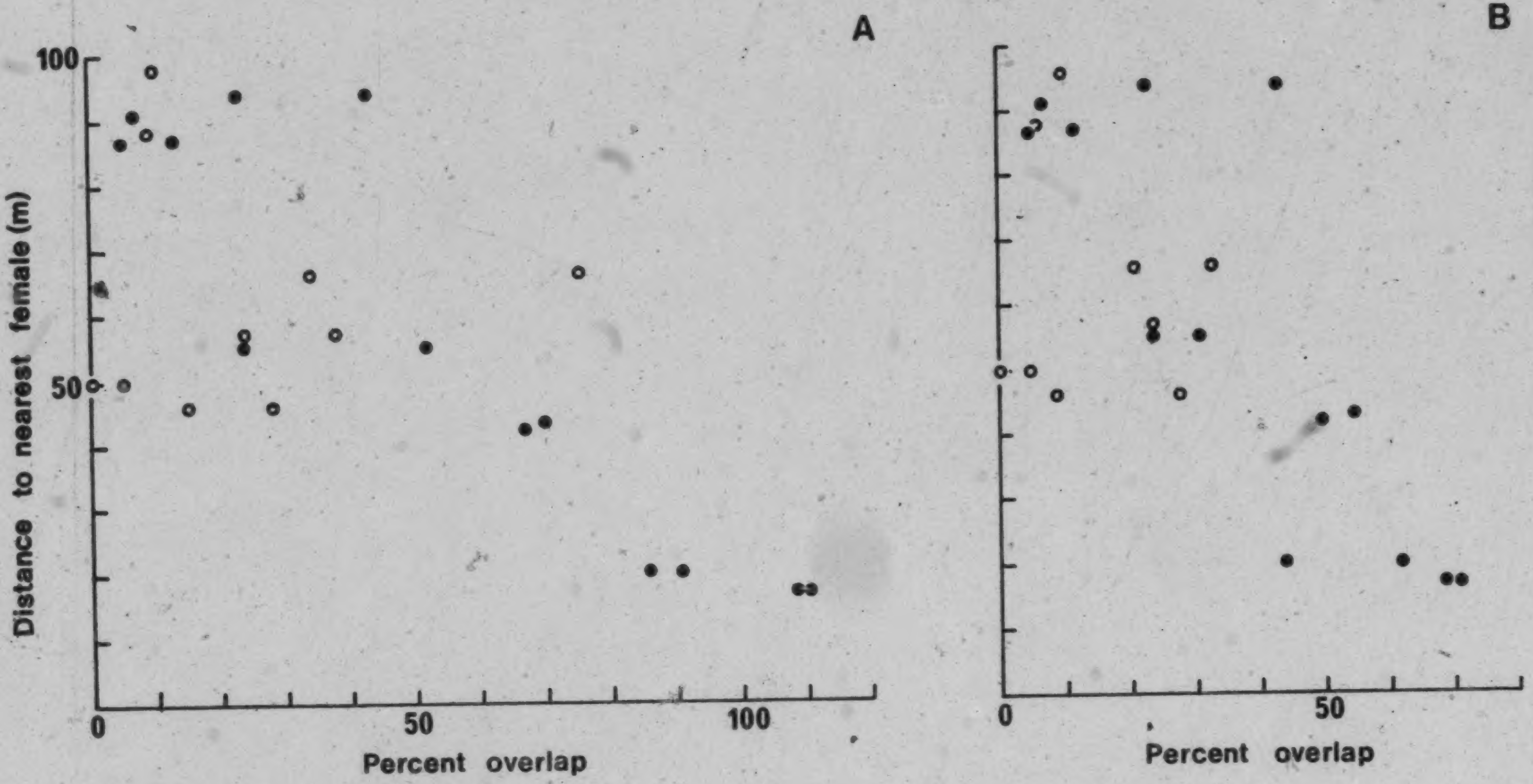


Fig. 13. Scattergrams show the relationship between an index of density (distance to nearest female) and the amount of the female's home range which it shares with (a) all neighbouring males, (b) only the male with which she appeared to be paired.

- ● Data for late summer 1970
- o Data for late summer 1971.

data from late summer was used since this was when there was least overlap and when the effect of large home ranges of males was minimal. Using Spearman's rank correlation it was found that there was a significant correlation in 1970 for all males, and paired males only. There were no significant correlations in 1971, but when the data for the two years were pooled the correlation was again significant.

The correlation coefficients and levels of significance for these analyses are shown in Table 11. The reason for the lack of correlation in 1971 is probably due to the sex ratio being skewed in favour of males, meaning that the distance to the nearest female gave a poor index of density for that year; also several of the paired females had died by that time and had not been replaced.

In summary, pikas appear to have a spatial organisation which disperses the adults in pairs. These pairs maintain relatively exclusive home ranges with respect to neighbouring animals. During the breeding season, adult males have a greater propensity to intrude into neighbouring ranges, and as a result, females may come into contact with more males during the breeding season than at other times of the year. There is a tendency for males and females to use separate parts of a mutually shared range,

Table 11. Spearman's rank correlation statistics on data from Fig. 13

		No. of pairs.	Correlation coeff.	T value.	df	Probability.
1970	Overlap between females and all males.	13	0.855	5.486	11	<0.001
	Overlap between females and paired male only.	13	0.806	4.521	11	<0.001
1971	Overlap between females and all males.	10	0.079	0.21	8	Not Sig.
	Overlap between females and paired male only.	9	0.095	0.25	7	Not Sig.
Total Both Years	Overlap between females and all males.	23	0.604	3.393	21	<0.01
	Overlap between females and paired male only.	22	0.581	3.199		<0.01

and this becomes more pronounced later in the summer and also at lower densities. This suggests that at higher densities they are forced to share space more than at lower densities. It appears that there may be a separate class of unpaired males, but this was not true for females. Variations from this general pattern, described earlier, suggest that the system can be modified if the circumstances (such as mortality) permit.

Male - Male Spacing

There were fourteen males on Area I during 1970 but by spring 1971 the number had risen to nineteen. The amount of overlap between these animals is shown in Tables 12 and 13. The matrices (set out for seasonal comparison) reflect a decrease in density from left to right and top to bottom. These data show the following trends. (1) There appears to be a steady decrease in the area of overlap with decreasing density. (2) The amount of overlap both in actual and percentage of area appears to be higher in 1971 than in 1970. (3) There is clearly a greater amount of overlap in early summer, as compared with late summer. These three trends were examined statistically in further detail.

Using the distance to the nearest male as an index of density, the percentage overlap of each male's home

Table 12. Matrix showing relative amounts of overlap between home ranges of individual males on Area I, 1970.

Percent of home range overlapped by other males

Early summer

	RY	RR	WN	GW	RG	GG	YK	NN	YR	BR	YW	BY	RN	NK
RY	**	23	-	-	7	-	-	-	-	-	-	-	-	-
RR	25	**	46	-	19	-	-	-	-	-	-	-	-	-
WN	-	21	**	5	3	-	-	-	-	-	-	-	-	-
GW	-	-	8	**	3	1	-	-	-	-	-	-	-	-
RG	15	39	11	8	**	19	15	-	-	-	-	-	-	-
GG	-	-	-	3	12	**	29	-	-	-	-	-	-	-
YK	-	-	-	-	13	39	**	2	-	-	-	-	-	-
NN	-	-	-	-	-	-	1	**	8	-	-	-	-	-
YR	-	-	-	-	-	-	-	10	**	-	-	-	-	-
BR	-	-	-	-	-	-	-	-	-	**	-	-	-	-
YW	-	-	-	-	-	-	-	-	-	-	**	-	-	-
BY	-	-	-	-	-	-	-	-	-	-	-	**	-	5
RN	-	-	-	-	-	-	-	-	-	-	-	2	**	-
NK	-	-	-	-	-	-	-	-	-	-	-	-	-	**
Total squares occupied by male														
	52	57	26	39	113	74	99	41	52	33	34	62	+	20

Late summer

	RY	RR	WN	GW	RG	GG	YK	NN	YR	BR	YW	BY	RN	NK
RY	**	10	17	2	-	-	-	-	-	-	-	-	-	-
RR	14	**	2	-	6	-	-	-	-	-	-	-	-	-
WN	19	2	**	2	-	-	-	-	-	-	-	-	-	-
GW	-	-	2	**	10	2	-	-	-	-	-	-	-	-
RG	-	8	-	15	**	2	-	-	-	-	-	-	-	-
GG	-	-	-	2	2	**	31	-	-	-	-	-	-	-
YK	-	-	-	-	-	26	**	9	-	-	-	-	-	-
NN	-	-	-	-	-	-	10	**	3	-	-	-	-	-
YR	-	-	-	-	-	-	-	2	**	-	-	-	-	-
BR	-	-	-	-	-	-	-	-	-	**	-	-	-	-
YW	-	-	-	-	-	-	-	-	-	-	**	-	-	-
BY	-	-	-	-	-	-	-	-	-	-	-	**	-	-
RN	-	-	-	-	-	-	-	-	-	-	-	-	**	-
NK	-	-	-	-	-	-	-	-	-	-	-	-	-	**
Total squares occupied by male														
	36	48	40	47	62	60	51	53	35	64	96	85	7	59

+Insufficient data

Table 13. Matrix showing relative amount of overlap between home ranges of individual males on Area I, 1971.

Percent of home range overlapped by other males

Early summer

	YB1	RY	RR	WN	GW	RG	BW1	GG	YK	ȲB	WW1	ȲR	BR	WK	YW	BY	WY	NK	YN
YB1	**	48	11	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
RY	48	**	17	5	14	6	9	-	-	-	-	3	-	-	-	-	-	-	-
RR	5	23	**	-	16	15	23	-	-	-	-	11	-	-	-	-	-	-	-
WN	-	2	-	**	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GW	-	12	10	14	**	18	18	-	-	-	-	6	-	-	-	-	-	-	-
RG	-	10	17	-	32	**	60	3	-	-	-	21	-	-	-	-	-	-	-
BW1	4	13	25	-	32	58	**	5	-	-	-	12	-	-	-	-	-	-	-
GG	-	-	-	-	-	3	4	**	20	33	33	-	-	-	-	-	-	-	-
YK	-	-	-	-	-	-	-	25	**	33	24	18	-	-	-	-	-	-	-
ȲB	-	-	-	-	-	-	-	5	4	**	-	1	-	-	-	-	-	-	-
WW1	-	-	-	-	-	-	-	18	11	-	**	-	-	-	-	-	-	-	6
ȲR	-	4	11	-	9	19	12	-	18	11	-	**	10	-	-	-	-	-	-
BR	-	-	-	-	-	-	-	-	-	-	-	3	**	-	-	-	-	-	-
WK	-	-	-	-	-	-	-	-	-	-	-	-	-	**	7	-	-	-	-
YW	-	-	-	-	-	-	-	-	-	-	-	-	-	18	**	-	-	-	-
BY	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**	27	-	-
WY	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15	**	8	-
NK	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15	**	-
YN	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	**
Total squares occupied by male	52	52	71	21	44	79	77	61	73	9	33	72	20	22	59	60	33	64	15

(continued)

Table 13, continued

Percent of home range overlapped by other males

Late summer

	YB1	RY	RR	WN	GW	RG	BW1	GG	YK	Y̅B	WW1	Y̅R	BR	WK	YW	BY	WY	NK	YN
YB1	**	18	14	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RY	43	**	10	11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RR	29	9	**	18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WN	14	9	17	**	-	-	--	-	-	-	-	-	-	-	-	-	-	-	-
GW	-	-	-	-	**	4	-	-	-	-	-	-	-	-	-	-	-	-	-
RG	-	-	-	-	11	**	6	3	-	-	-	-	-	-	-	-	-	-	-
BW1	-	-	-	-	-	7	**	-	-	-	-	-	-	-	-	-	-	-	-
GG	-	-	-	-	-	4	-	**	17	-	46	-	-	-	-	-	-	-	-
YK	-	-	-	-	-	-	-	18	**	-	23	-	-	-	-	-	-	-	-
Y̅B	-	-	-	-	-	-	-	-	-	**	-	-	-	-	-	-	-	-	-
WW1	-	-	-	-	-	-	-	15	7	-	**	-	-	-	-	-	-	-	3
Y̅R	-	-	-	-	-	-	-	-	-	-	-	**	-	-	-	-	-	-	-
BR	-	-	-	-	-	-	-	-	-	-	-	-	**	-	-	-	-	-	-
WK	-	-	-	-	-	-	-	-	-	-	-	-	-	**	-	-	-	-	-
YW	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**	-	-	-	-
BY	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**	13	-	-
WY	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	**	-	-
NK	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**	-
YN	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-	-	-	-	**
Total squares occupied by male	14	33	29	27	9	28	35	39	40	?	13	40	52	?	30	51	23	22	30

?Animal disappeared from population.

range was plotted against this index (Fig. 14). This was done using data from 1970 and 1971 taken during late summer when overlap was minimal. Spearman's rank correlations were found to be significant in each year and combined years (Table 14). This indicates that with increasing density home ranges become less and less exclusive, however no animals were overlapped more than 100 percent indicating that in late summer, all animals were able to maintain at least part of their home range for their exclusive use (with respect to other males). Since there is this difference in overlap with density one would expect a greater amount of overlap in 1971 than 1970, the population of males being higher in 1971. Indeed, using a Mann-Whitney U test a significant difference was found in the amount of overlap between males in early summer ($P < 0.025$), but not during late summer. The lack of significance for late summer is probably due to a small sample size since examination of Fig. 14 shows that the animals with the four highest amounts of overlap are all from 1971. Additionally, the two animals on the extreme right of the graph, with the overlap of 77 and 86 percent were both yearling unpaired males born in 1970.

Seasonal differences in the degree of home range overlap were significant also. Home ranges of males overlapped significantly more in early summer than late summer

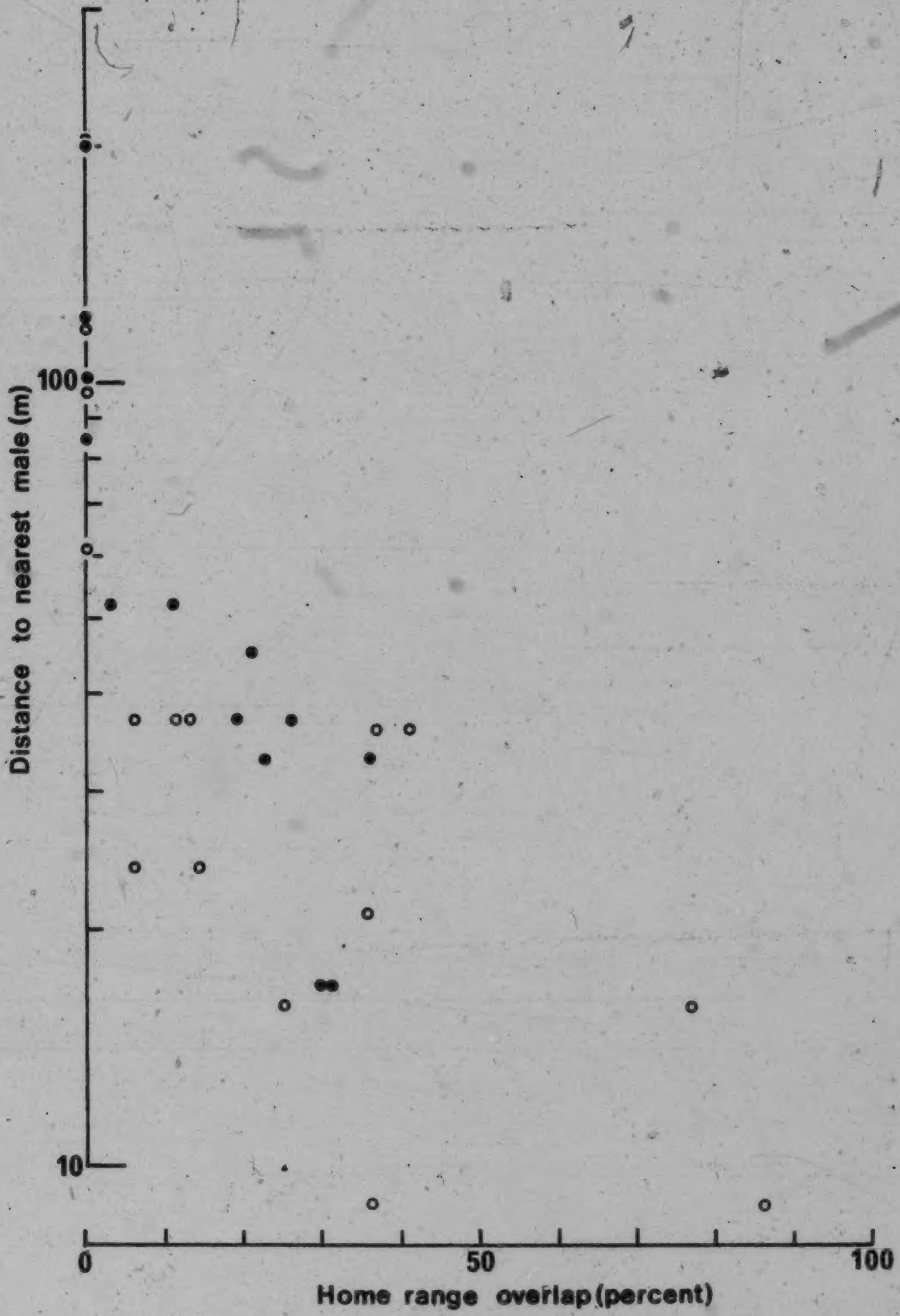


Fig. 14. Scattergram showing relationship between overlap of male home ranges and density. Late summer on Area I.

● Data for 1970

○ Data for 1971

Table 14. Spearman's rank correlation statistics on data from Fig. 14.

	No. of animals in sample	Correlation coeff.	T value	df	Probability
1970 Overlap among males	13	0.901	6.892	11	<0.001
1971 Overlap among males	17	0.829	5.755	15	<0.001
Both Years	30	0.841	8.273	28	<0.001

(1970, $P < 0.005$; 1971, $P = 0.01$ - Wilcoxon's signed ranks test). These differences corresponded with the larger size of home ranges of males in early summer. One interesting feature here is that there were four males which did not show a decrease in home range overlap later in the summer, and of these four, three were unpaired yearling males. This suggests that unpaired males might show different seasonal changes in use of space than do paired males.

Among mature paired males relative dominance between animals may be reflected in their home range characteristics. This is illustrated in Figs. 15 and 16. Home ranges of five adjacent males on Area I in late summer are shown in Fig. 15 and overlap was generally small, although in one case quite large (YK v GG). The situation in early summer (Fig. 16) showed a much larger amount of overlap. However examination of the ranges showed almost all the overlap was a result of range extensions by three of the males - RY, RG, and YK. These three not only overlapped their neighbours completely but maintained larger exclusive areas than RR and GG; the latter showed almost no range extension. All these animals were paired and all at least two years of age. Further, the same pattern was apparent in 1969 though the number of observations are fewer and GG and RR were unpaired at that time. This suggests that if pikas are considered as being territorial, there may be relative dominance among them, giving some

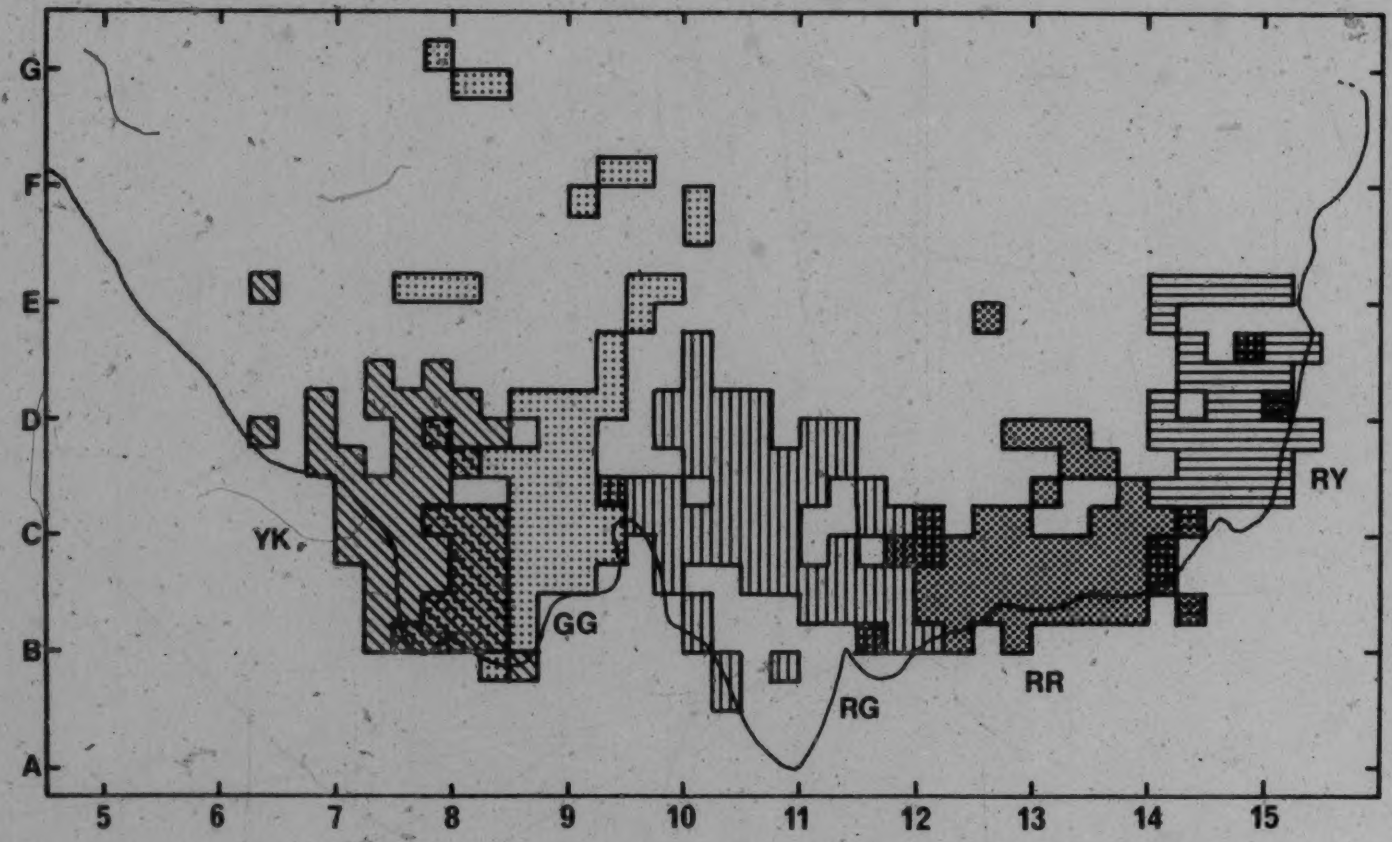

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Fig. 15. Relationship among the home ranges of five adjacent males during late summer 1970. All animals were paired with females. Number of observations: YK = 266, GG = 226, RG = 184, RR = 208, RY = 138.

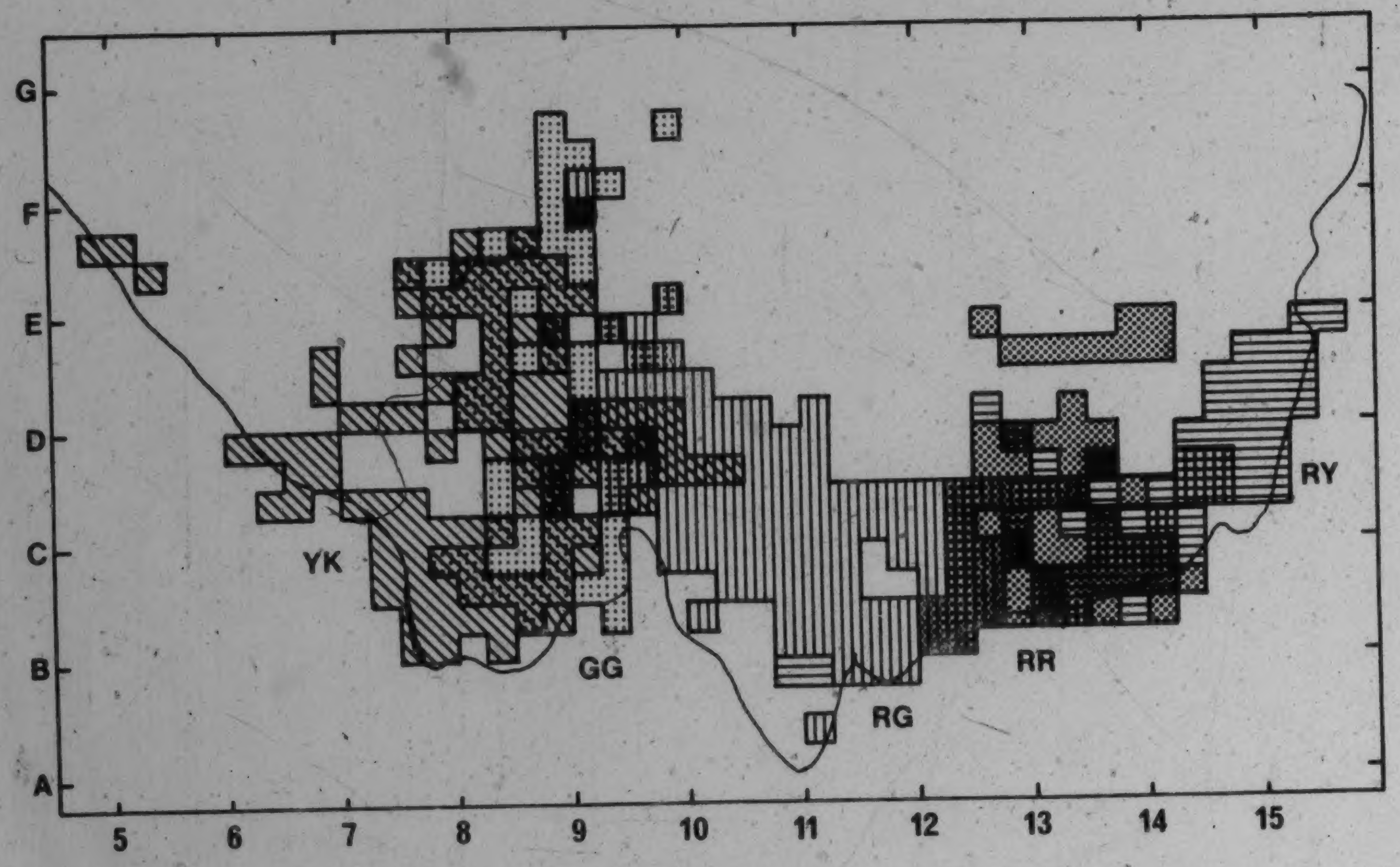
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Fig. 16. Relationship among the home ranges of five adjacent males during early summer 1970. Number of observations: YK = 222, GG = 146, RG = 255, RR = 219, RY = 167.

individuals the capacity to intrude into other territories while the more subordinate individuals do not reciprocate.

Female - Female Spacing

In this section spacing among females is analysed in a similar fashion to the male - male analysis, and the results are then compared with those of males.

The overlap among females on Area I during 1970 and 1971 is shown in Tables 15 and 16. There were few apparent differences between seasons or years though there again appeared to be a correlation with density, particularly during 1970. This is shown in Fig. 17. Spearman's rank correlation for 1970 was significant, but this was not true in 1971; when both years were combined the data were again significant (Table 17). The lack of significance in 1971 could have been due to loss of several females living in the area of highest density.

Seasonal comparisons were made using Wilcoxon's signed ranks tests, and in both years there were no significant seasonal differences in home range overlap. This agrees with the analysis of home range size in females which showed no seasonal differences.

In general, it appeared that females had home ranges which were fairly exclusive and yet like males, tended to overlap with increasing density. Moreover,

Table 15. Matrix showing relative amounts of overlap between home ranges of individual females on Area I, 1970.

Percent of home range overlapped by other females

Early summer

	RK	KB	KY	RB	KK	GB	KW	RW	GK	KG	GY	BB	WB
RK	**	32	-	-	-	-	-	-	-	-	-	-	-
KB	62	**	4	8	-	-	-	-	-	-	-	-	-
KY	-	2	**	2	-	-	-	-	-	-	-	-	-
RB	-	12	8	**	-	-	-	-	-	-	-	-	-
KK	-	-	-	-	**	12	-	-	-	-	-	-	-
GB	-	-	-	-	13	**	-	-	-	-	-	-	-
KW	-	-	-	-	-	-	**	17	-	-	-	-	-
RW	-	-	-	-	-	-	11	**	-	-	-	-	-
GK	-	-	-	-	-	-	-	-	**	-	-	-	-
KG	-	-	-	-	-	-	-	-	-	**	-	-	-
GY	-	-	-	-	-	-	-	-	-	-	**	-	-
BB	-	-	-	-	-	-	-	-	-	-	-	**	-
WB	-	-	-	-	-	-	-	-	-	-	-	-	**
Total squares occupied by female	29	57	26	87	45	50	36	23	12	+	41	25	+

Late summer

	RK	KB	KY	RB	KK	GB	KW	RW	GK	KG	GY	BB	WB
RK	**	40	-	-	-	-	-	-	-	-	-	-	-
KB	62	**	3	-	-	-	-	-	-	-	-	-	-
KY	-	2	**	-	-	-	-	-	-	-	-	-	-
RB	-	-	-	**	3	-	-	-	-	-	-	-	-
KK	-	-	-	1	**	14	-	-	-	-	-	-	-
GB	-	-	-	-	29	**	2	-	-	-	-	-	-
KW	-	-	-	-	-	1	**	16	-	-	-	-	-
RW	-	-	-	-	-	-	11	**	-	-	-	-	-
GK	-	-	-	-	-	-	-	-	**	-	-	-	-
KG	-	-	-	-	-	-	-	-	-	**	-	-	-
GY	-	-	-	-	-	-	-	-	-	-	**	-	-
BB	-	-	-	-	-	-	-	-	-	-	-	**	-
WB	-	-	-	-	-	-	-	-	-	-	-	-	**
Total squares occupied by female	29	45	34	67	31	65	54	37	27	108	83	42	66

+Insufficient data.

Table 16. Matrix showing relative amounts of overlap between home ranges of individual females on Area I, 1971.

Percent of home range overlapped by other females

Early summer

	RK	KB	KY	RB	KW	RW	$\overline{N}N$	KG	GY	NG	BB	$\overline{Y}Y$	WB
RK	**	9	-	-	-	-	-	-	-	-	-	-	-
KB	15	**	-	1	-	-	-	-	-	-	-	-	-
KY	-	-	**	1	-	-	-	-	-	-	-	-	-
RB	-	3	4	**	-	-	-	-	-	-	-	-	-
KW	-	-	-	-	**	9	-	-	-	-	-	-	-
RW	-	-	-	-	6	**	-	-	-	-	-	-	-
$\overline{N}N$	-	-	-	-	-	-	**	2	-	-	-	-	-
KG	-	-	-	-	-	-	4	**	-	-	-	-	-
GY	-	-	-	-	-	-	-	-	**	-	-	-	-
NG	-	-	-	-	-	-	-	-	-	**	-	-	-
BB	-	-	-	-	-	-	-	-	-	-	**	-	-
$\overline{Y}Y$	-	-	-	-	-	-	-	-	-	-	-	**	-
WB	-	-	-	-	-	-	-	-	-	-	-	-	**
Total squares occupied by female	20	33	27	78	52	34	19	25	47	9	26	30	23

Late summer

	RK	KB	KY	RB	KW	RW	$\overline{N}N$	KG	GY	NG	BB	$\overline{Y}Y$	WB
RK	**	-	-	-	-	-	-	-	-	-	-	-	-
KB	-	**	-	-	-	-	-	-	-	-	-	-	-
KY	-	-	**	-	-	-	-	-	-	-	-	-	-
RB	-	-	-	**	-	-	-	-	-	-	-	-	-
KW	-	-	-	-	**	6	-	-	-	-	-	-	-
RW	-	-	-	-	6	**	-	-	-	-	-	-	-
$\overline{N}N$	-	-	-	-	-	-	**	-	-	-	-	-	-
KG	-	-	-	-	-	-	-	**	-	-	-	-	-
GY	-	-	-	-	-	-	-	-	**	-	-	-	-
NG	-	-	-	-	-	-	-	-	-	**	-	-	-
BB	-	-	-	-	-	-	-	-	-	-	**	6	-
$\overline{Y}Y$	-	-	-	-	-	-	-	-	-	-	11	**	3
WB	-	-	-	-	-	-	-	-	-	-	-	3	**
Total squares occupied by female	?	?	29	33	34	33	39	17	20	?	18	35	32

[?] Animal disappeared from population.

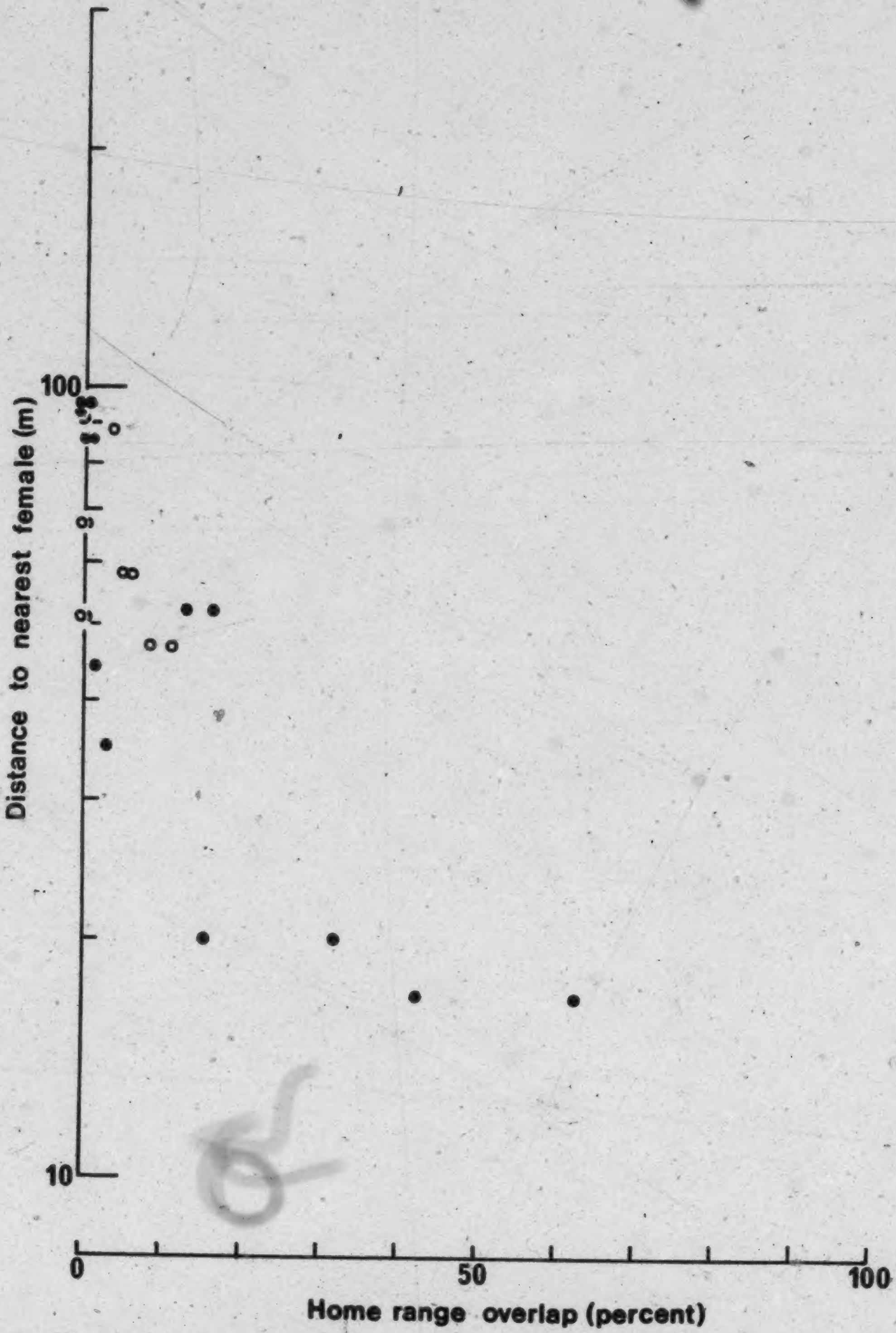


Fig. 17. Scattergram showing relationship between overlap of female home ranges and density. Late summer on Area I.

● Data for 1970

○ Data for 1971.

Table 17. Spearman's rank correlation statistics on data from Fig. 17.

	No. of animals in sample	Correlation coeff.	T value	df	Probability
1970 Overlap among females	13	0.8365	5.0637	11	<0.001
1971 Overlap among females	10	0.4303	1.3483	8	Not Sig.
Both years	23	0.6783	4.2309	21	<0.001

these home ranges did not change seasonally in terms of size or amount of overlap. There was no indication that there was a separate class of unpaired individuals among females, as there was in males.

Statistical comparison of overlap among males versus among females was complicated by the correlations with density already shown. This means that where sample sizes were grossly unequal there were likely to be differences in density which could account for differences in overlap. Further, even when sample sizes were fairly close, the relative density (as indicated by nearest neighbour distances) for males and females may be quite different depending on the dispersion of animals within the population. The results of these comparisons of overlap are shown in Table 18. In early summer the overlap among males was significantly higher than among females; this was true for 1971, and 1970 and 1971 combined. The difference was not significant in 1970. In late summer there were significant differences in 1971 and combined years, but these were likely due to large discrepancies in sample sizes rather than differing tendencies among males and females.

Considering the sample sizes, it seems that males and females show the same degree of spatial exclusion among members of their own sex, except during early summer

Table 18. Statistical comparisons, using Mann-Whitney U test, of the overlap among females' home ranges compared with overlap among males' home ranges.

			Average home range overlap	Significance level
Early summer				
1970	Males	(13)*	30.3%	Not. Sig.
	Females	(11)	16.6%	
1971	Males	(19)	56.5%	P<0.001
	Females	(13)	3.5%	
Both years	Males	(32)	45.9%	P<0.001
	Females	(24)	9.5%	
Late summer				
1970	Males	(14)	14.3%	Not Sig.
	Females	(13)	14.0%	
1971	Males	(17)	23.0%	P<0.005
	Females	(10)	1.4%	
Both years	Males	(31)	19.1%	P<0.05
	Females	(23)	8.6%	

*Number of animals in sample.

when males extend their home ranges, and except when there are many 'bachelor' males in the population.

In summary, the spatial pattern of male pikas is much more variable both seasonally and individually than that of females. Despite these major differences between the sexes, individual males and females were often closely related in terms of space, suggesting a system of pairing. This means that the two systems are probably interrelated and should not be considered as separate systems operating independently of one another.

POPULATION LEVELS

Area I was the only population which was studied continuously throughout the three year period, where the population itself was well defined and on which no experimental manipulations were done. Changes in population levels are shown in Fig. 18, and since all animals were individually marked, complete cohorts could be followed throughout the study. During 1969 not all adults were marked and the spring figure and number of juveniles that year may have been slightly underestimated. In 1972 only one week was spent on the study area and again it is not certain whether a complete census was obtained, although it is probably close to the real figure.

The population of adults showed a gradual increase from 1969 to 1971 but appeared to drop in 1972. Along with this increase from 1969 to 1971, there was a change in the sex ratio as mentioned earlier (Table 8). Although there was this slight change in numbers the population as a whole seemed to be stable and there was no evidence from this study area or any of the others that pikas showed large fluctuations in numbers.

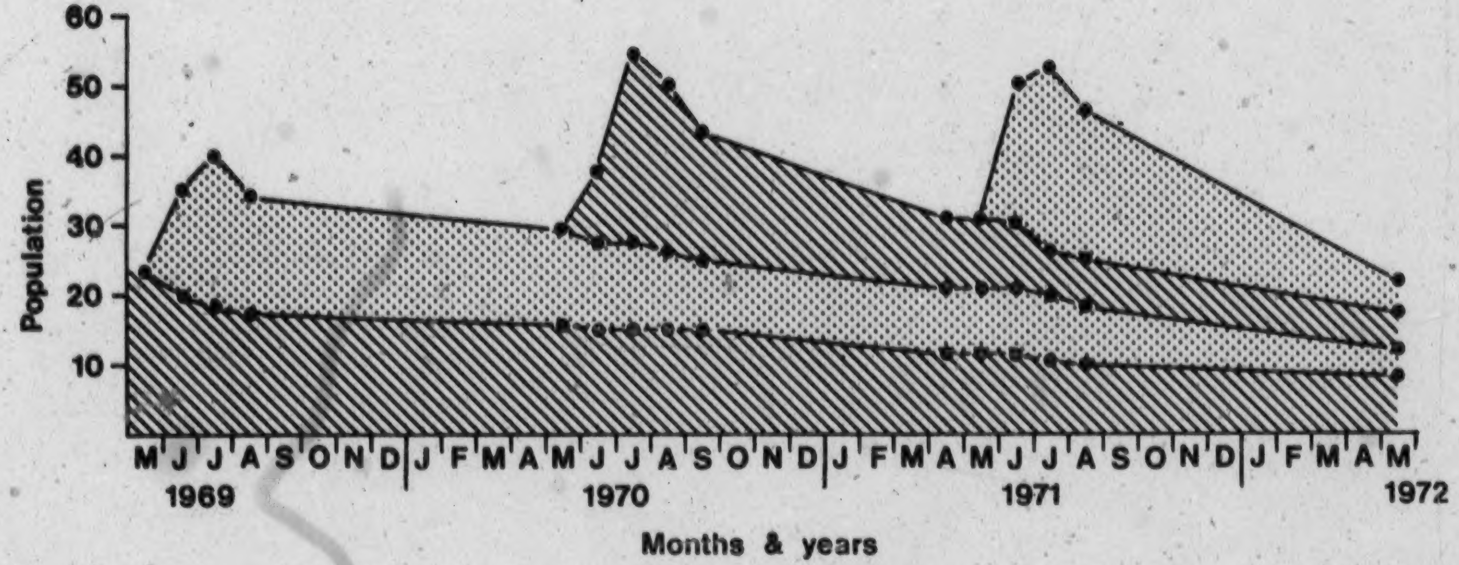


Fig. 18. Population levels on Area I, 1969 to 1972.

DISPERSAL AND SETTLEMENT

Dispersal

Howard (1960) defined dispersal as "the movement an animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate." Such a definition is unworkable in the present context since it is difficult to know whether an animal would have bred if it had survived; for example, animals moving onto marginal habitat may never breed. Also dispersal may not comprise a single movement but may have separate phases which take place at different times of the year. Finally, in this as in most field studies, it is difficult to know whether an animal's disappearance is due to death or dispersal. Therefore, for the purposes of this section, all shifts of home range will be considered, some may validly be described as dispersal, others may not. These movements will be considered under two headings; interpopulation movements and intrapopulation movements. This does not necessarily imply that different mechanisms are involved.

Interpopulation Movements

Evidence for these movements is scanty and largely circumstantial. The only way in which emigration was quantifiable in this study was through examination of rates of loss from the population. On Area I the rates shown in Table 19 were derived during the whole course of the study, and clearly much of this loss was also mortality. This shows that the loss of juveniles was much higher than that of either yearlings or adults, but it also indicates that yearlings had a higher rate of loss than adults. Whether this reflects a higher dispersal rate or a higher mortality rate among this group, is not clear.

There was no direct evidence of yearlings making interpopulation movements, but there was evidence of intrapopulation movements by yearlings, which suggests longer movements are possible. Although there was a correlation between age (up to 26 months) and the rate of loss per month (Spearman's rank correlation coefficient = 0.928; $P < 0.01$), the rates of loss shown in Table 19 indicate that the bulk of interpopulation movements are made by juveniles during the late summer of their birth.

Immigration also gives an idea of the relative rates of long distance dispersal although the rates will be far lower than the actual dispersal rates because of mortality during dispersal. A major problem is that unless one has the entire population (including every

Table 19. Disappearance rate of animals from Area I (1969 - 71), by age.

	Loss/month as percent of total					
	Early summer		Late summer		Winter	
No. of Months	2		2		8	
Juveniles	*	*	26/80	16.25%	17/35	6.07%
Yearlings	3/23	6.52%	2/20	5.00%	3/11	3.41%
Adults	3/37	4.05%	1/34	1.47%	2/15	1.66%

juvenile) marked, a new animal may represent one not marked but from within the population, rather than from outside. On Area I there were a number of animals which could have been immigrants; often they first appeared late in the season when all others were marked and had weights indicating they were several weeks old; others were found in spring when it was presumed that the entire population had been marked the previous autumn. There were 16 of these animals over three years of study, 9 were females, 3 were males and 4 were not sexed. On other areas, data were also scanty; Area II had one immigrant male between 1969 and 1970, before experimentation was begun. Area III had two immigrants during 1971, a male and a female. All of these animals appeared to have moved during the year of their birth though this was not always certain.

To obtain more information on interpopulation movements, and also to study settlement patterns of animals on new areas, animals were removed from two populations. All were removed from Area II during May 1971. This rockslide, which had previously held about two pairs of adults was then checked for immigrants every two weeks during the rest of summer. On August 12, 1971 a single juvenile was seen on the area, and later captured -- this animal had been tagged on Area I and was last seen there on July 25, 1971. The distance of this movement was almost three kilometres and involved crossing a mountain river about 15 metres wide; further, two low hills separated the two rockslides so that they were not visible one from the other, and most of the area between was pine forest. This animal was still present on Area II in May 1972 and appeared to be alone at that time.

On Area IV, a small section of talus, which in previous years contained 2 - 3 pairs of adults, was cleared of animals in June 1971. Although not a discrete area, since sections of talus inhabited by pikas were within two to three hundred metres, most immigrants would have had to make long dispersal movements to settle into the area. Two juvenile males and three juvenile females moved onto this area during August 1971.

These data suggest that juvenile animals of both sexes are involved in interpopulation movements, although there seems to be a higher proportion of females among these animals. This was also reported by Millar (Appendix I).

Intrapopulation Movements

On Area I juveniles could usually be caught within a few days of emergence from the nest and their movements followed within the population. The distances of all movements of juveniles of known sex are summarised in Table 20.

Table 20. Summary of dispersal movements during late summer on Area I 1969-1971. Distances are from birth site or point of first capture to location of settlement. Animals which disappeared or moved off the study area are excluded.

Distance moved (metres)	Males	Females
0 - 19	9	6
20 - 39	10	2
40 - 59	7	2
60 - 79	1	2
80 - 99	1	1
120 - 139	0	1
140 - 159	0	1
160 - 179	0	1
180 - 199	0	1
300 - 319	0	1
340 - 359	0	2
360 - 370	0	1

The distances are direct measurements from birth site (if known) or point of first capture, to the location of settlement -- this was usually indicated by the establishment of a haypile. The dispersal pattern of females was different from that of males, indeed using a G test (equivalent to Chi-square) the distributions differed significantly ($P < 0.05$). There was a high tendency for males to stay within a few metres of their birth site. This was not true for females, although a higher number were recorded in the shortest movement category.

It is possible that some of the animals whose birth sites were not known came from outside the population. In this category there were six females of which one moved 90 metres, and the others all moved less than 50 metres from the point of first capture. The two males in this category both moved less than 20 metres from the point of first capture.

Settlement and Replacement

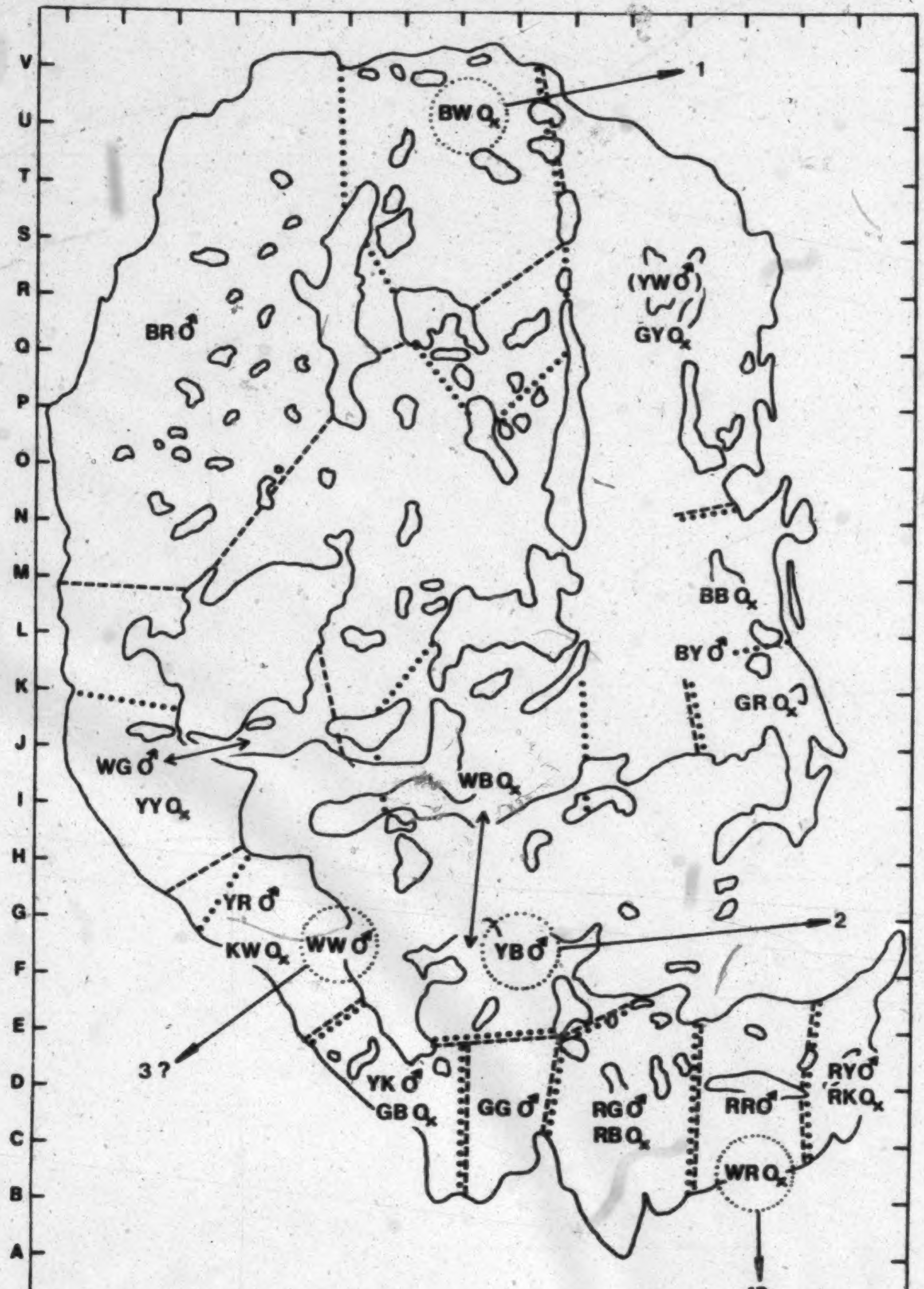
If social behaviour in the form of territoriality is regulating the population, settlement of animals into that population should relate directly to the number and location of losses from the established population. Figs. 19 to 25 show changes in the established population on Area I and the dispersal patterns of juvenile animals within it. On the basis of the studies of home range and spatial organisation presented earlier the established

Fig. 19. Population of adults on Area I during summer of 1969. Data interpreted as a paired territorial system.

---------Boundaries between males.

••••••••••••Boundaries between females.

1. Female died in trap July 13.
2. Male died in trap May 22.
3. Male disappeared - last seen June 2.
4. Female disappeared - last seen May 24.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RG ♂
RB ♀x
RR ♂
RY ♂
RK ♀x
WR ♀x
4?

Fig. 20. Dispersal movements of all tagged juveniles on Area I during summer 1969.

● Approximate position of birth site.

_/ Point of first capture.

▲ Place of settlement.

? Details of birth site not known; or animal disappeared before end of summer.

1. Animal not found here until 1970.

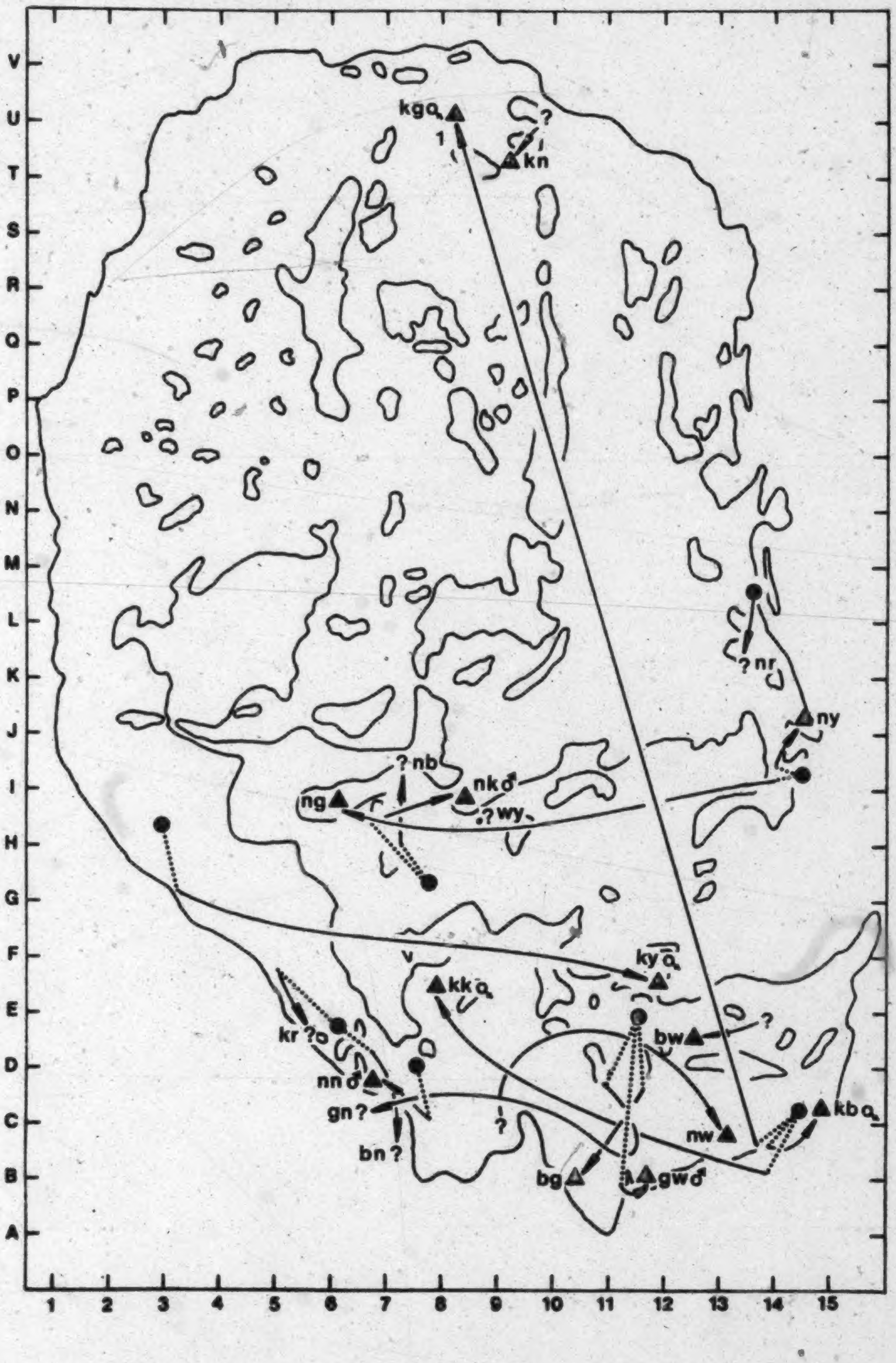
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Fig. 21. Population of adults on Area I during summer of 1970.

1. Female disappeared - last seen May 15.
2. Male (NN), had moved to new location by May 1.
3. Male (GW), had moved to new location by May 1.
4. Male disappeared - last seen July 18.

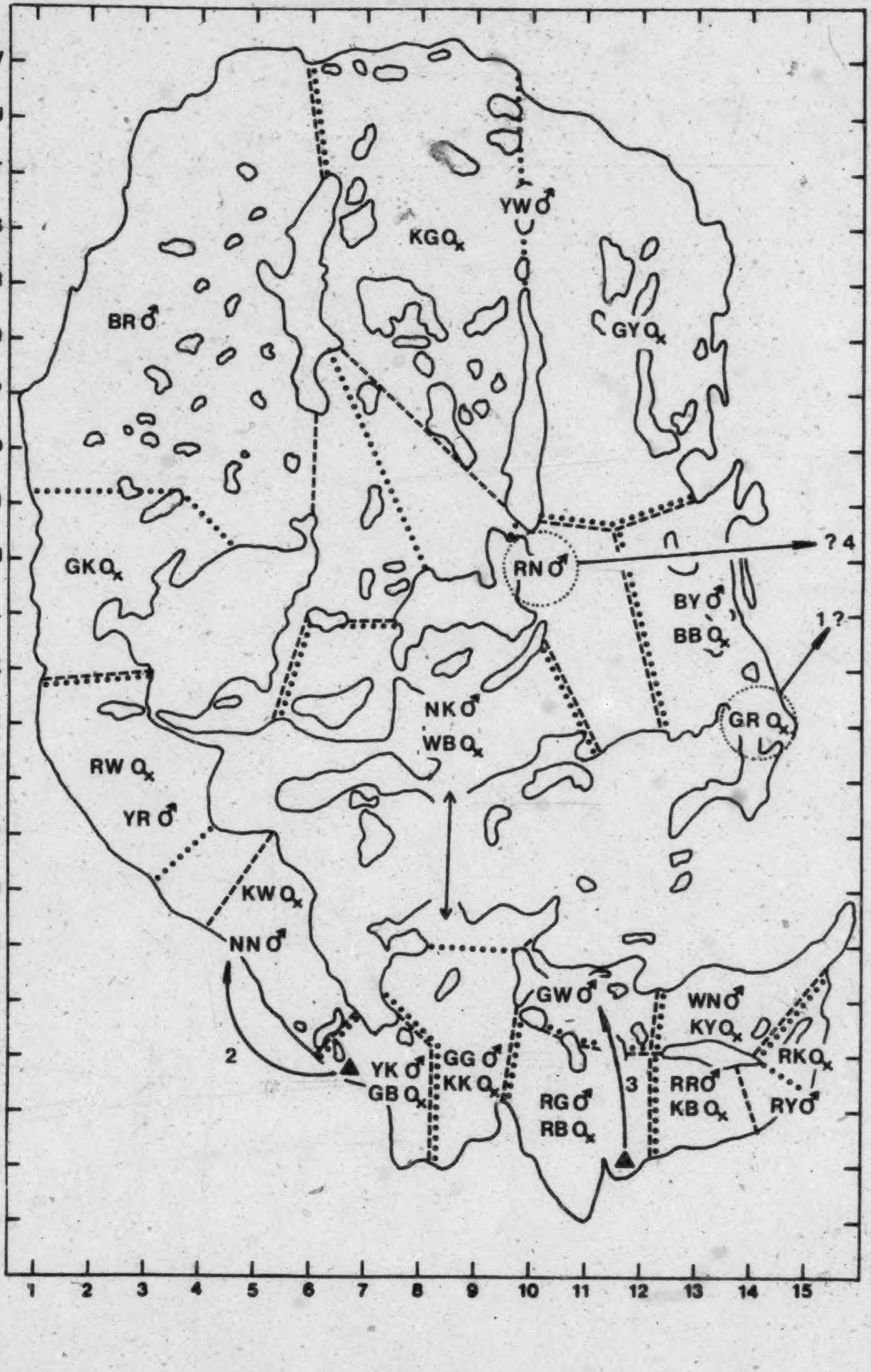
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Fig. 22. Dispersal movements of all tagged juveniles on Area I during summer 1970.

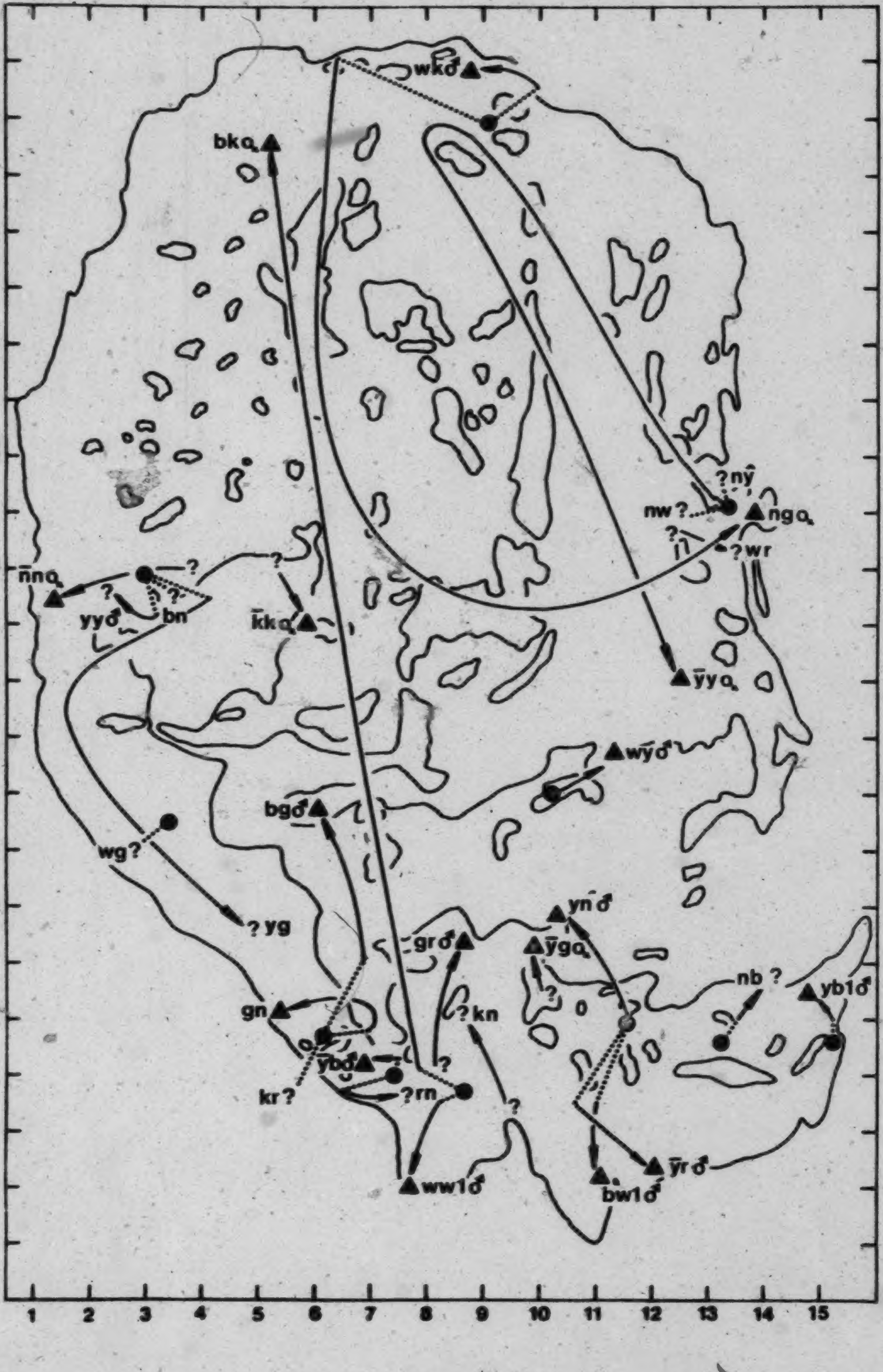
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Fig. 23. Population of adults on Area I during summer of 1971.

1. Male disappeared - last seen May 1.
2. Female disappeared - last seen June 17.
3. Male (WW1) moved by April 26, but later disappeared - last seen July 11.
4. Male disappeared - last seen May 1.
5. Male ($\overline{Y}$R) moved between May 1 and May 6.
6. Female disappeared - last seen June 13.
7. Female disappeared - last seen June 20.

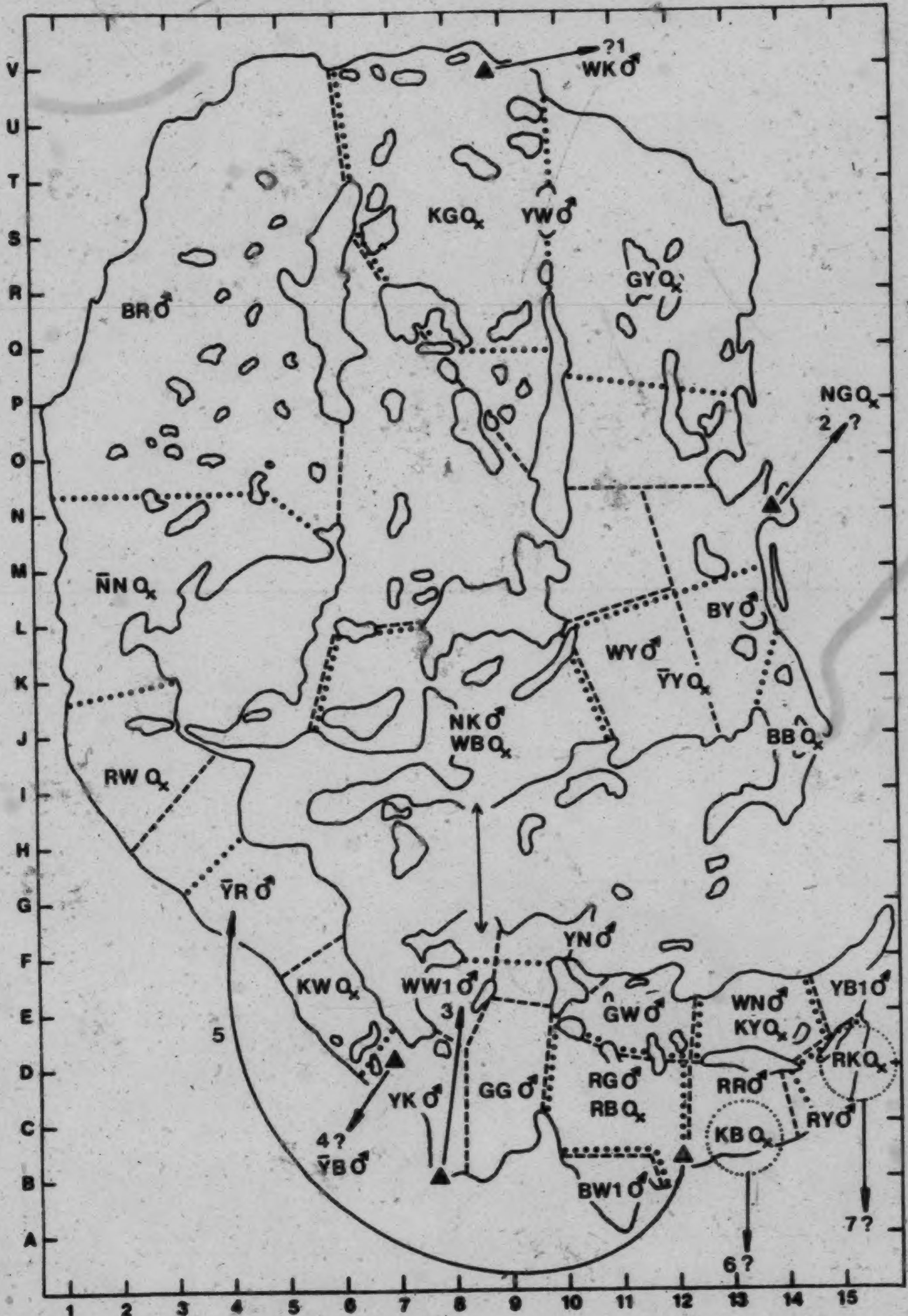
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Fig. 24. Dispersal movements of all tagged juveniles on Area I during summer of 1971.

1. Male last seen on Area I, July 25; reappeared on Area II, August 12 1971.

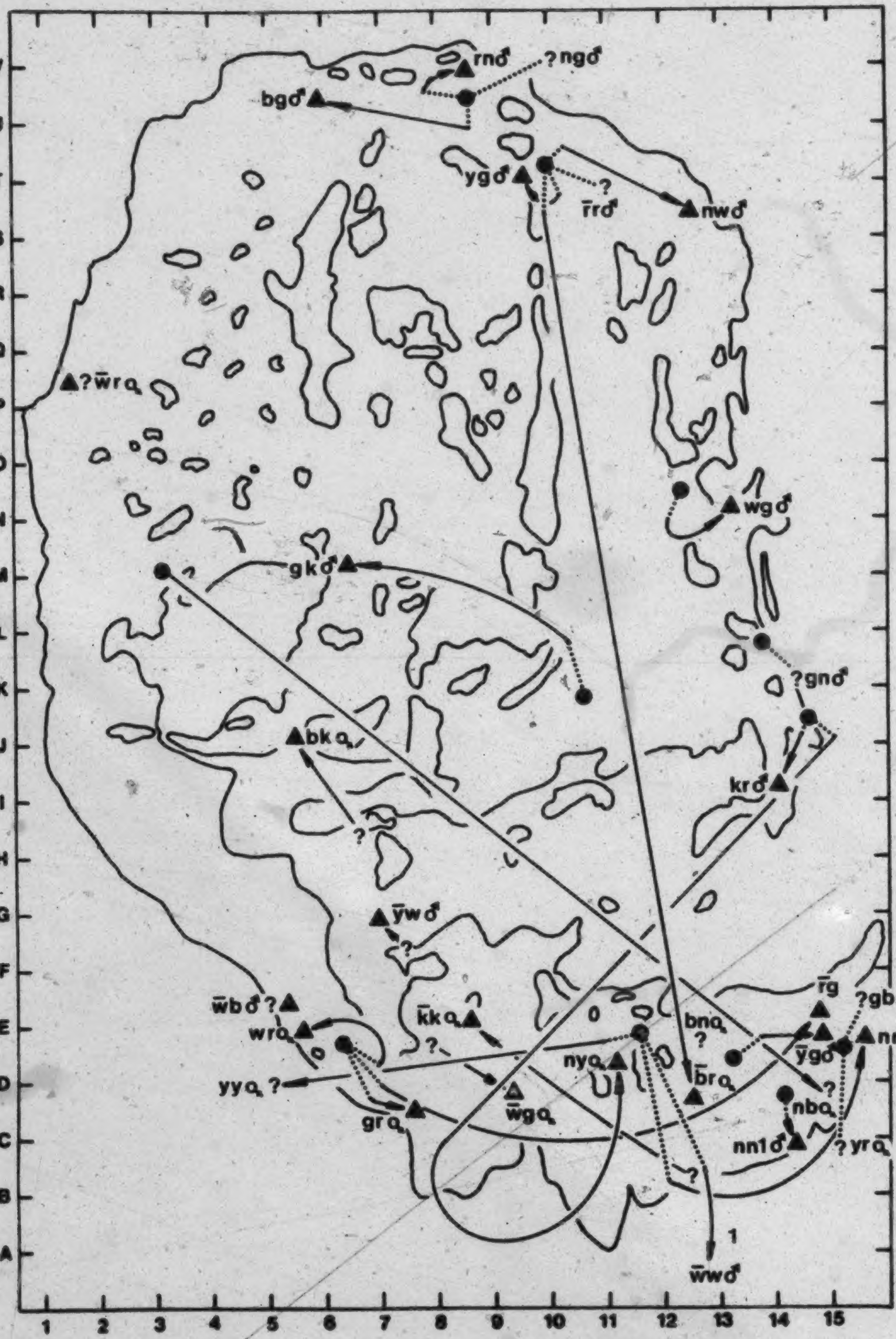
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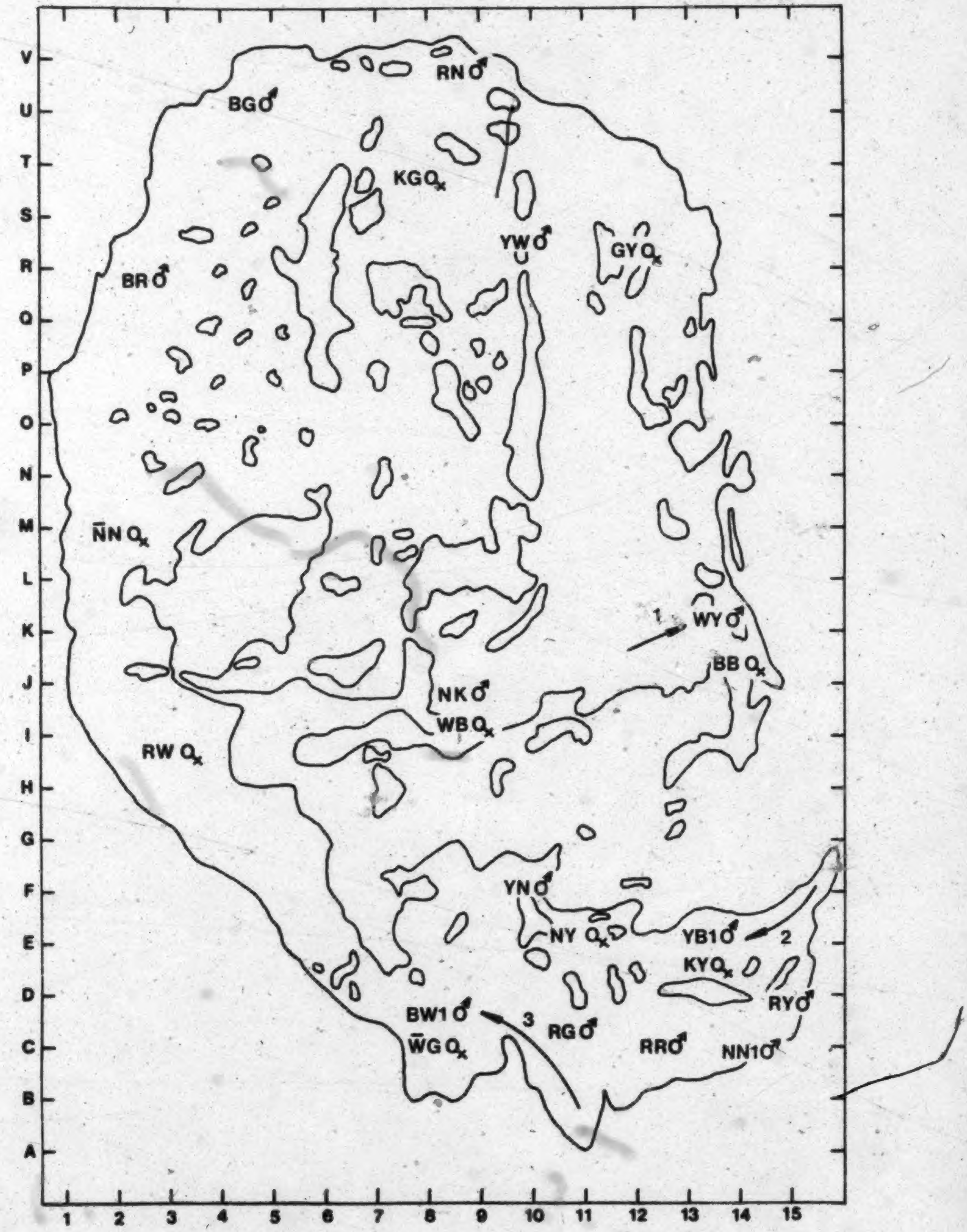
Fig. 25. Approximate locations of adults on Area I at end of May 1972. Census may not be complete.

1. Male WY appeared to have shifted to replace lost male BY.
2. Male YBl appeared to have shifted to replace lost male WN.
3. Male BWl appeared to have shifted to replace lost males YK and GG.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BG♂
KG♀
YW♂
GY♀
BR♂
N̄N♀
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WY♂
BB♀
NK♂
WB♀
RW♀
YN♂
NY♀
YB1♂
2
KY♀
RY♂
BW1♂
3
RG♂
W̄G♀
RR♂
NN1♂

population is interpreted as being a paired territorial system, with some minor variations. Boundaries are simplified for clarity and are of course subject to my interpretation.

The dispersal movements of juveniles show the tendency of males to stay close to their birth site or move relatively short distances, and the tendency of females to make both short and longer movements before settling. Using these data, settlement patterns will be related to dispersion of adults.

1. Settlement in a saturated population.

In 1970 the population along the lower edge of the slide appeared to be saturated -- movements of two yearling males (NN and GW) probably took place earlier in the spring (Fig. 21). All animals were paired except one yearling male (GW) and all these individuals survived the entire summer. Fig. 22 shows the movements and settlement of juveniles in that year. Only one female settled into this population (Y̅G) and this could be related to the unpaired male GW, or to other juvenile males settling close by. Characteristically, the males produced in this population also settled within it; there were seven of them and most appeared to have moved short distances only. By the following spring, the only new female (Y̅G) had gone and so had one of the seven new males (this male was found dead in May 1971). Two of the remaining six males moved, ȲR shifting to a new location where an adult male had been lost, and ȲB moving slightly before disappearing at the end of May. The other males survived, effectively increasing the population of males by four, but all remained unpaired and the population of breeding pairs actually declined through the loss of two adult females (GB and KK) -- Fig. 23.

Only one of the juveniles which settled in this area could have been an immigrant (female ȲG).

2. Settlement where females are lost.

The lower edge of Area I just examined produced different results the following year (Fig. 23). Two of the adult females were lost during the winter of 1970-71 and two more were lost during the summer of 1971. Fig. 24 shows the dispersal of juveniles during that year. Four juvenile males settled in the area (ȲG, NN, ȲW, W̄B), in a similar pattern to the year previously, but a total of seven females settled (NR, BR, NY, KK, WG, GR, WR), compared with only one the previous year. Several of these females moved considerable distances into this part of the slide.

There were other instances where juvenile females dispersed and replaced lost females. For example, a female (BW) was killed in a trap in 1969 (Fig. 19) but was replaced by KG (Fig. 20). In other situations the loss and replacement took place later or earlier than the periods of study -- RW replacing YY (Fig. 21) and N̄N replacing GK (Fig. 22).

3. Settlement where males are lost.

Over the winter of 1970-71 two males (YR and NN) were lost (Figs. 21 and 23). Both males adjacent to them expanded their home ranges, particularly in the spring, and perhaps as a result of this, both of the remaining females bred. One of the lost males was replaced by a yearling (ȲR) in May 1971 (Fig. 23), but only one juvenile moved onto this area during that year (W̄B) and it did not survive until 1972.

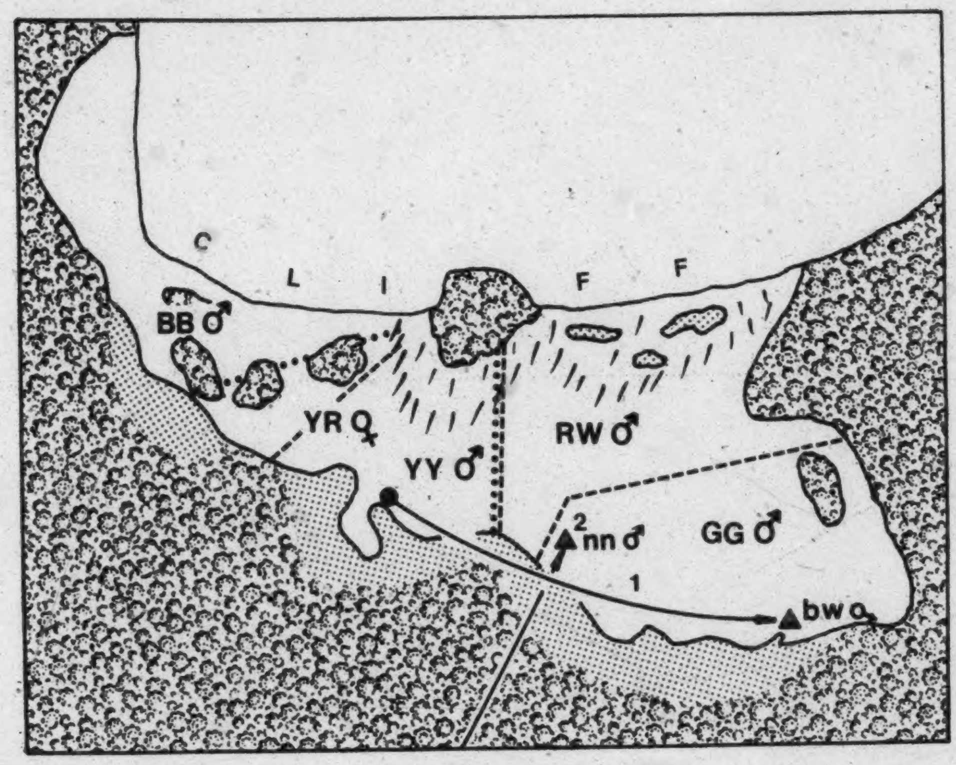
Replacement of adult males may not always be by juveniles, but sometimes by marginal, unpaired males. The most striking example of this was shown on Area II between 1969 and 1970 (Fig. 26). On this area, in spring 1969, the female which was paired with GG was lost and later replaced by a juvenile female (BW); the only other pair on the area was YY and YR, with RW and BB representing marginal males. A single immigrant juvenile male (NN) settled on the slide -- first seen at the end of September 1969. Over winter, male YY disappeared and was replaced by RW who in turn was replaced by NN giving the situation

Fig. 26. Replacement sequence on Area II, late summer 1969 (a) to spring 1970 (b).

------------ Boundaries between males.

.... Boundaries between females.

1. Dispersal movement of juvenile female.
2. Immigrant juvenile male.
3. Male YY is lost and is replaced by male RW who is in turn replaced by NN.


C
L
I
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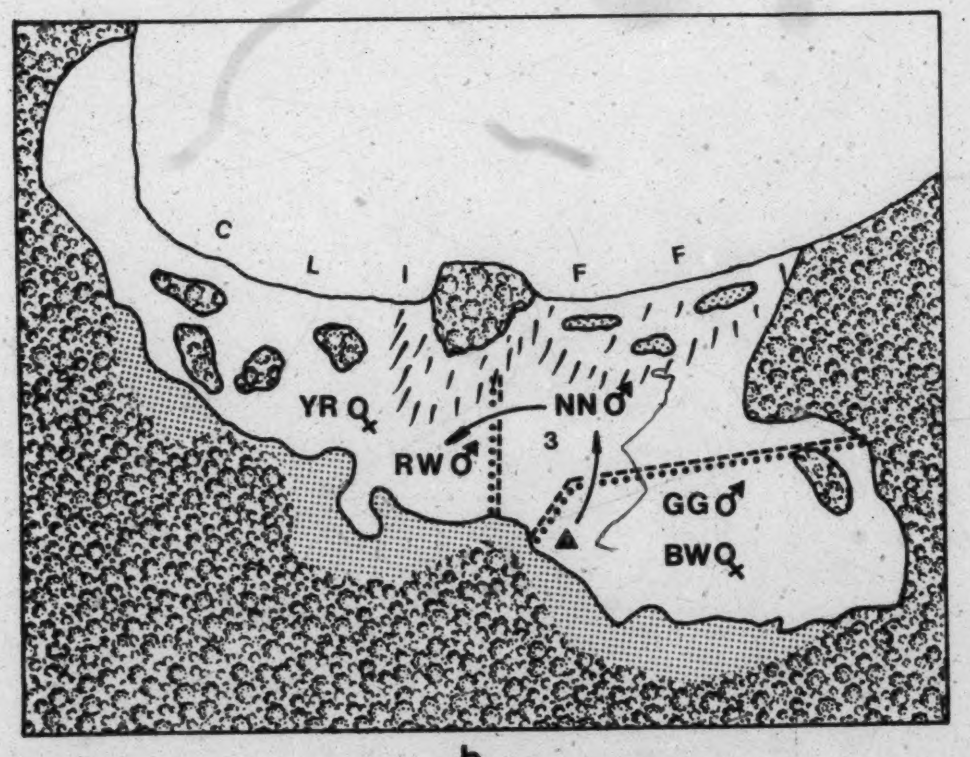
BB ♂
YR ♀
YY ♂
RW ♂
2
nn ♂
GG ♂
1
bw ♀

a


C
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RW ♂
GG ♂
BW ♀

b

in Fig. 26(b). Similar events appeared to have taken place on Area I between 1971 - 1972 (Fig. 23 and 25). This may be the reason for males taking up marginal situations, where the likelihood of securing a mate may be small.

4. Settlement on areas where all pikas are lost.

In two removal experiments, sections of talus were cleared of pikas to study settlement patterns on uninhabited areas. On Area II only a single male settled and it took up a small home range around one of the previous haypile sites. On Area IV, where a section of talus, which normally contained about five adults, was depopulated, replacement was by two males and three females. This occurred in an interesting sequence: all adults were removed during June; on July 7 a juvenile male was shot mistakenly -- it was thought to be a resident previously not noticed, but appears to have been an immigrant; no more animals were seen until July 27 when a second juvenile male was captured and tagged; by July 31 a female moved onto the area and at once established close to the male; two other females had moved onto the area by August 14; both settling close to the male.

This sequence suggests that males may move into new areas first and be followed by females shortly afterwards.

BEHAVIOURAL INTERACTIONS

In spite of the high amount of overlap among home ranges of males during the early part of the year, the number of interactions observed between animals was relatively small. Table 21 summarises numbers of physical interactions (fighting and chasing) seen in 1970 and 1971 on Area I. These usually involved only chases, and on one or two occasions only were animals actually seen to make contact. There was frequent chasing between males and females just prior to copulation and some of the encounters recorded may have been of a precopulatory type. For comparative purposes the number of encounters must be related to the frequency of observations, since the latter varied considerably from period to period.

Although the data were generally too few to be of much significance several trends were indicated.

1. There was a general decline in the frequency of encounters between adult males as the summer progressed. This corresponded with the decrease in home range overlap between them.

2. Females almost never chased other females.

Table 21. Summary of the number of physical encounters (fights and chases) seen between various age and sex classes of pikas on Area I, 1970-71. These are compared with total numbers of observations.

	Interactions						Observations		
	MvM	FvF	MvF	JvJ	MvJ	FvJ	Males	Females	Juveniles
1970									
May	1	0	4	-	-	-	514	275	-
June	10	0	11	1	0	0	1043	531	27
July	1	2	11	0	5	1	946	697	224
Aug-Sept	0	0	2	2	16	3	1104	940	538
1971									
May	6	0	5	-	-	-	1117	346	-
June	6	0	2	0	0	0	712	389	130
July	4	0	3	0	2	0	845	308	413
Aug	0	0	0	0	4	1	331	105	199

M = adult male, F = adult female, J = juvenile.

3. Males and females interacted throughout most of the summer though there appeared to be a slight decline in August. This may have corresponded with the tendency of pairs to separate spatially later in the summer.

4. Encounters involving juveniles increased later in the season, corresponding especially with the period of settlement of young animals.

DISCUSSION

The objective of this study required that the main emphasis be placed on dispersion or spacing patterns of pikas, and the dispersal and settlement of juveniles to determine how they were affected by this adult pattern. The emphasis was on the animal's use of space and little attention was paid to other components of behaviour. The discussion will involve some of the problems inherent in studying spacing systems and their causes, and then will evaluate the data obtained in this study to determine the nature of the dispersion and dispersal patterns. Finally, consideration will be given to how the system could affect the recruitment of young animals and how this in turn may affect population levels.

Spacing Systems - Concepts and Problems.

The concept of territory, used primarily in connection with spacing mechanisms in birds (Howard 1920), has been defined in two ways. Noble (1939) described it as a defended area, implying, as Kaufman (1971) pointed out, that it is primarily a behavioural phenomenon whereas Pitelka (1959) using the word in an ecological sense, suggested it should be considered as an exclusive area. Clearly, animals could be territorial under one definition but not under the other. Burt (1943) suggested that mammals are likely to have home ranges which overlap and territories within them that are defended.

Field studies of various mammals have revealed spacing mechanisms which are often difficult to define in terms of territoriality, yet may have elements which suggest it -- such as exclusive areas and spatially related aggression. Grubb and Jewell (1966) showed that groups of Soay sheep had overlapping home ranges but maintained monopolised zones within them -- though there was no evidence of defence. Kaufman (1962) in a study of coatis (Nasua) found that groups had core areas which overlapped other home ranges but which never overlapped the core areas of other groups. Perhaps the most striking example was shown by Leyhausen (1965) in feral domestic cats which had home ranges which overlapped, yet animals used the common areas at precisely different times, suggesting a kind of 'temporal territory.'

Partly as a result of these complexities, there has been a tendency to define various types of territory among animals. In birds for example, Nice (1941) recognised six types, but rigidly followed Noble's definition; in mammals, Fisler (1969) described three basic types with eight subtypes. This array of patterns makes it difficult to define territory as a clear concept which includes a single unifying principle: a purely arbitrary definition is pointless and in this case misleading since the word is in such wide use (eg. Ardrey 1966). Also, as Emlen (1957) pointed out, use of the word may imply characteristics to an animal, not all of which have been clearly established; further, to describe an animal as non-territorial may imply it has no spacing mechanisms at all. Because of the problems some authors still use the term though do not define it, and use it in a general sense rather than as a specific phenomenon -- Carpenter (1958) considered territoriality as a "....behavioural system expressed in a spatial temporal frame of reference," but did not define it precisely; similarly Kaufman (1971) suggested that "....no simplified definition or explanation of territory yet advanced can cover all of the related kinds of behaviour known, and perhaps it is naive to look for one." Brown and Orians (1970) on the other hand kept to a rigid definition but interpreted the word defence in a very wide sense so as to include not only attacking, chasing and threatening, but also display, 'certain vocalizations' and scent marking; having defined it in a behavioural sense they further qualify it in an ecological sense, stating that if defence fails to keep the area exclusive it should not be considered as territoriality.

Tinbergen (1957), taking another approach to the problem, pointed out that territoriality was basically the outcome of two different behavioural tendencies, namely site attachment and hostility. Clearly if these two tendencies are variable, various combinations will give a multitude of outcomes which may or may not be defined as territory. Indeed Fisler (1969) used these two basic tendencies to classify all dispersion patterns in mammals, outcomes being selected for in relationship to such proximate factors as habitat, population density, and food supply. Population density does appear to alter the social system; Anderson (1961) suggests that house mice (*Mus*) show a territorial system at low densities but a hierarchical system at high densities and Lockie (1966) suggests almost the opposite in weasels (*Mustela*), where at low densities animals tend to be transitory.

However, because the word territory has been so widely used it is almost impossible to avoid using the term, particularly since authors frequently present their data on the basis of territorial interpretations. I shall use the term here in its widest sense -- as used by Car[illegible]nter (1958), but try to explain variations in spacing in terms of differing degrees of hostility and site attachment rather than as different types of territory.

Spatial Organisation of Pikas

The spatial pattern of home ranges, the nature of home ranges, and the dispersal and settlement patterns of young animals were studied. Some differences were found between areas of high and low density, and also between seasons. At this stage I will try to evaluate the findings and present a picture of the spatial pattern to show how these aspects could be integrated into a structured social system.

The adult population of pikas was spaced so that animals were living essentially as pairs of males and females. Pairs had home ranges which corresponded in size with the density of individuals; on areas of high density home ranges were small and cramped together whereas at low densities home ranges were much larger and more spread out. Although these regional differences may be affected by other environmental factors, the amount of vegetation on feeding areas was high in the areas of high density, suggesting that food supply may be a factor of major importance in the dispersion of the adult population. At differing densities the spatial arrangement of animals varied slightly; at high densities males and females shared almost all of the space available, although there was a tendency, particularly late in the summer, for them to use different parts of this range; at low densities the home ranges of males and females were often separate to a large extent, although never completely -- suggesting a paired relationship was still maintained. Although sizes of home ranges were related to density the amount of overlap between neighbours was greater at high densities than at lower densities. However, even at high densities most adult animals managed to maintain part of their home range exclusively for their own use. These tendencies suggest pikas have behavioural mechanisms for maintaining exclusive areas but that these become less effective at higher densities.

Seasonal changes in this adult pattern were mainly found among males. In the early part of the summer, during the breeding season, the overlap among males was very high and some animals were unable to maintain exclusive areas; this increase in overlap was due to an increase in the home range size of males, some members of the population showing this more than others. These range extensions increased the overall proportion of talus area within most home ranges. Chasing among males was also most frequent at that time. Later in the summer home ranges were more exclusive and chasing diminished. Such results clearly indicate territorial tendencies among males, but too narrow an interpretation of the word territory is confusing and may be misleading. For instance, defined as an exclusive area, after Pitelka (1959), one would conclude pikas were territorial during the late summer, but not in the spring; whereas defined as a defended area (Noble 1939) one would perhaps conclude the opposite since there is more fighting in spring. Furthermore, such restrictive interpretations may overlook important details; for example, the amount of overlap among males in early summer suggested that certain males were more dominant than others and could intrude into neighbouring territories, while more subordinate animals were not able to do this. This was further indicated by the outcome of some fights, in which an intruding dominant would sometimes chase a resident neighbour in the latters' own territory. Such interactions were more evident on high density than on low density areas. This suggests, along with greater amounts of overlap, that with increasing density a relatively simple territorial system becomes modified to show elements of a social hierarchy.

In females there was little seasonal difference in size of, and overlap among home ranges, but there was the same correlation of home range overlap and density that was shown in males. Home ranges of males and females were very similar in late summer, in both size and amount of overlap.

If seasonal changes in home ranges of males are interpreted with respect to site attachment and hostility, evidence suggests that site attachment increased from early to late summer (smaller home ranges; increased intensity of use of central portion in late summer; haypile construction etc.), whereas hostility decreased (fewer chases between adult males) as the summer progressed. Interestingly, the model proposed by Fisler (1969) does not allow for such a possibility, since he shows these tendencies as being correlated. However, such factors are likely to be important in the pika, particularly with respect to dispersal and settlement of young, since juvenile males were able to settle into saturated areas during late summer, but by the following spring had to move -- due perhaps to their own lower site tenacity and partly due to the increased hostility of surrounding males.

Spacing of adults could have occurred in several ways, but three possible alternatives are:-

1. Separate spacing systems by males and females both operating independently, and the females presumably more effective than males, since their home ranges were more exclusive.

2. A single spacing system for both sexes, where females perform the main spacing role and males merely follow the pattern set by females.

3. A single system where primary spacing is

determined by males, and females follow this pattern.

The first possibility appears the least likely since there is evidence from the dispersion and home ranges of adults, and settlement of juveniles, that males and females associate in pairs -- thus effectively integrating the spatial pattern of males and females.

Two pieces of evidence favour the second possibility, firstly the high degree of exclusion shown in home ranges of females, and secondly the direct replacement of lost females by juvenile females (this, however, is often ambiguous since in most cases it could have been interpreted as pairing with the remaining male rather than avoiding other females). The mechanism by which such spacing could be accomplished is not clear since actual encounters were very infrequent between adult females, and more covert methods such as avoidance have to be postulated.

The third possibility, that of spacing by males appears the most likely since overt mechanisms, such as chasing , are apparent in the early summer. Against this must be set the evidence that home ranges of males overlapped in early summer, and that juvenile males settled into saturated populations during late summer. However the high degree of overlap in early summer could be the cause of the fighting and this may be interpreted as territorial intrusion at a time of the year when territorial boundaries are being reasserted and disputed. Furthermore, the movements of yearling males in early summer strongly suggest that they have shifted as a response to this increased pressure. Why they were allowed to settle as juveniles is not clear, but it is possible that haypile construction is more important to adults in late summer than is territorial integrity.

If spacing is indeed accomplished by males, then home ranges of females should be interpreted as being within the territories of established males. Thus overlap between females would be minimal. Finally, in this explanation, I do not preclude the possibility of hostility and spacing mechanisms in females. I only suggest that most of the spacing in pika populations is brought about by the action of territorial males.

The manner in which juveniles fitted into the established pattern can be shown best as a series of options. In males these appeared to be:

1. Move a short distance to, (a) a place in 'prime' habitat just big enough to construct a haypile but which likely involves defending the site against neighbouring adults, or (b) move to a 'marginal' area close by.

2. Disperse from the population, with the probability of colonizing other areas of suitable habitat.

Option one appeared preferable to option two, if space was available. If a juvenile took the first option and survived until spring some rearrangement usually occurred; (1) an animal in prime habitat could force neighbouring adults to make large scale readjustments to accommodate it; or, more likely, (2) it was forced to move to marginal areas, or move to fill vacancies left by adult mortality; or (3) it could be forced to leave the population. An animal in marginal habitat, if it survived, was likely to either remain in position or move into better habitat to replace a lost adult.

For juvenile females, movements appeared to be confined to late summer, most animals dispersing to replace lost females within the population, or moving from the population entirely. Sometimes they settled with males in marginal habitat, but this was infrequent. It is also possible that juveniles may displace adults from the population. There were two cases where this could have happened in females, but the evidence was circumstantial. Kawamichi (1971) suggested this possibility in Ochotona hyperborea but gave no details.

Fig. 27 is a diagrammatic summary of the replacement patterns of a generalised pika population.

The social system of the pika in Alberta can be

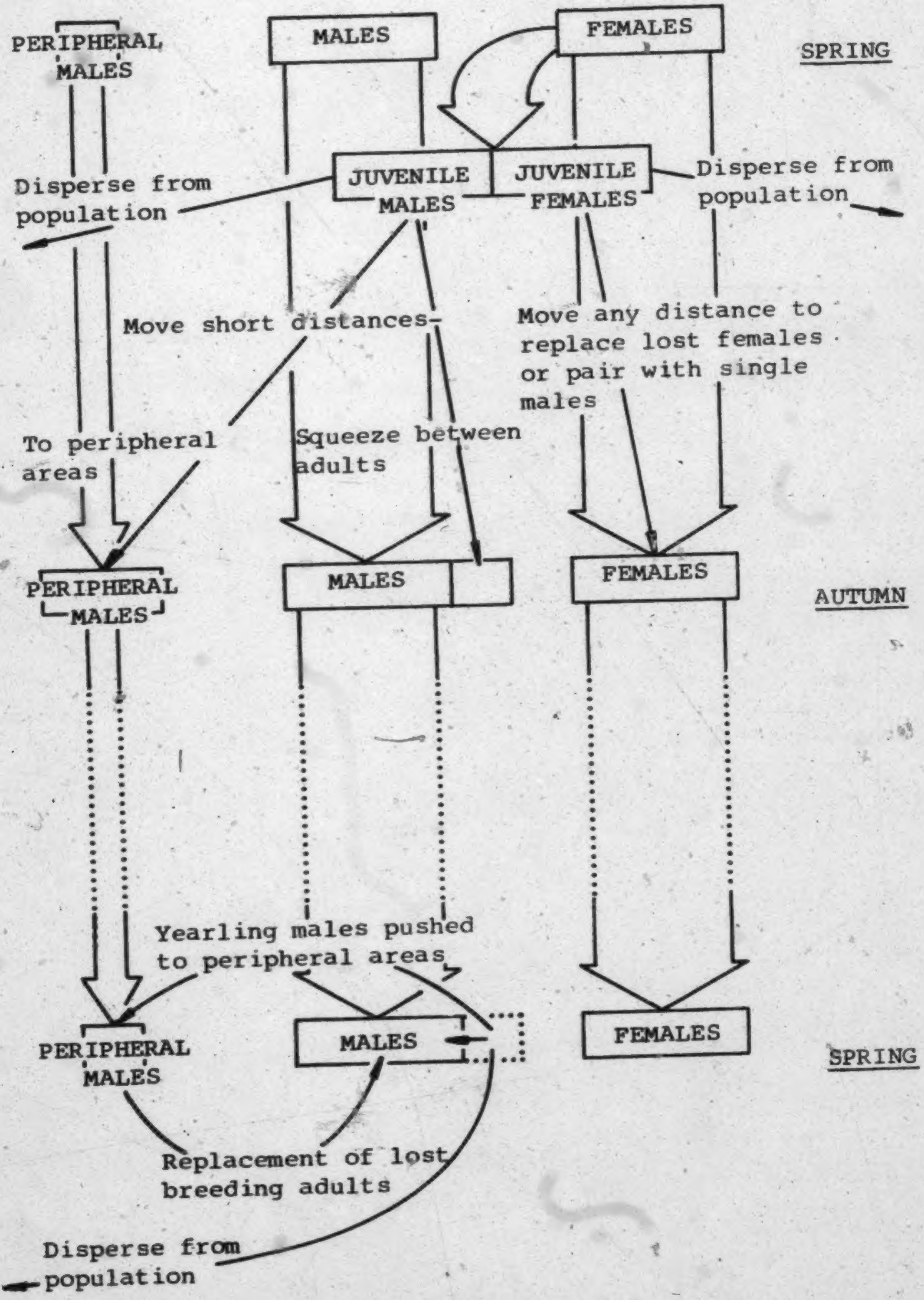
PERIPHERAL MALES
MALES
FEMALES
SPRING
Disperse from population
JUVENILE MALES
JUVENILE FEMALES
Disperse from population
Move short distances
Move any distance to replace lost females or pair with single males
To peripheral areas
Squeeze between adults
PERIPHERAL MALES
MALES
FEMALES
AUTUMN
Yearling males pushed to peripheral areas
PERIPHERAL MALES
MALES
FEMALES
SPRING
Replacement of lost breeding adults
Disperse from population

Fig. 27. Model showing differences of dispersal and settlement between males and females.

compared with only a few other studies on Ochotona princeps. Kilham (1958), Krear (1965) and Broadbooks (1965) suggested territoriality among pikas and Broadbooks suggested that some animals may be more dominant than others; however he was not able to capture animals and therefore was unable to confirm sex or age. Krear also suggested territoriality for the pika in Colorado on the basis of site dependent aggression. He concluded that pikas lived in pairs during the early summer but separated into a territorial arrangement during the latter half of the summer -- unfortunately he presented no data on spatial organisations so comparisons are not possible. Sharp (1973) suggested a similar system but was hesitant to describe pikas as territorial at any time of the year although she thought that they approached this condition in late summer. Severaid (1955) by contrast, found no evidence of territoriality among pikas because more than one animal could use the same burrow and home ranges appeared to overlap considerably -- again he presented little quantitative data upon which comparisons can be made.

Recent work on the Japanese pika (Ochotona hyperborea; Kawamichi 1969, 1970, 1971) has suggested that adults live essentially in pairs though occasional single individuals and groups of three were found together. Further, Kawamichi found that there was considerable home range overlap by males during early summer. He presented no data on dispersal, but suggested that animals of both sexes dispersed and that some displaced resident adults.

Of the other Lagomorpha, only the social system of Oryctolagus has been well documented (Mykytowycz 1958, 1959, 1960; Myers and Poole 1959, 1961; Mykytowycz and Gamble 1965). In this species the social organisation is more complex than that of pikas and consists of group territories within which rigid dominance hierarchies are established among males and females (Mykytowycz 1958). Home ranges of adult females were generally smaller than adult males, and as in pikas, increasing density caused home ranges to shrink (Myers and Poole 1959). Home ranges of dominant males were larger than subordinates, particularly during the breeding season, and aggression between males was always high. In females, there was little aggression except at higher densities (Myers and Poole 1961). Mykytowycz (1959) noticed adult males which were not associated with group territories but which nevertheless tried to usurp the positions of established dominant males. Mykytowycz (1968) emphasized the role of males in most of the territorial behaviour. In short, similar elements can be seen in the social organisations of pikas and rabbits except that in the latter the outcome is a considerably more complex arrangement. In Sylvilagus Marsden and Holler (1964) found a system similar to that of Oryctolagus except they argued that dominant males defended females rather than territory as such. Relatively little is known of the social system of hares and data is somewhat fragmentary (Lechleitner 1958; Rongstad and Tester 1971).

Social organisations of mammals have been extensively reviewed by others (Eisenberg 1965; Ewer 1968; Fisler 1969) and spacing systems appear to be generally unrelated to taxon. These systems range from individually territorial types such as pocket gophers (Thomomys, Howard and Child 1959) through animals which are partly territorial and dispersed in pairs such as mink and weasels (Mustela, Gerell 1970 and Lockie 1966) to complicated colonial systems such as occur in rabbits, ground squirrels (Spermophilus, Carl 1971) and prairie dogs (Cynomys, King 1955). Such wide variations may be explainable in terms of adaption of behavioural systems to differing habitats and environmental resources (Crook 1970, a, b). Although such evolutionary aspects are clearly important in the development of social systems, I shall only consider those aspects which pertain to the regulation of numbers.

Dispersal

Patterns of dispersal differed depending on the sex of the animal. Females made many intrapopulation movements and some interpopulation movements, whereas males made almost no intrapopulation movements in late summer but did make some long distance interpopulation movements

-- though it was not clear how many animals were usually involved.

Howard (1960) suggested that animals may have two types of dispersal mechanisms; an innate type which triggers dispersal regardless of surrounding social conditions, and an environmental type where the animal moves only in response to social pressure. Such mechanisms, he suggested, would help to explain the strong bimodality or skewness of dispersal distances in some studies. This hypothesis has been supported in recent studies by French et al. (1968), partially by Yeaton (1972) and notably by Myers and Krebs (1971) who found genetic differences between resident and immigrant populations. However, Murray (1967), in a theoretical model, showed the skewness could be explained by a single mechanism.

The results on dispersal of pikas could be explained by a single system for males and another for females. Males, characterized by a strong site tenacity, usually were able to remain very close to their birth site. However, increased hostility by surrounding adults could dislodge one, after which, being on unfamiliar ground, it could be quickly pushed from the population. Females, if they had a lower site tenacity, would move relatively easily but tend to disperse towards unpaired males rather than away from the population in general. More information on interpopulation movements is clearly needed.

Although these data could fit Howard's hypothesis, it does not seem necessary to explain them since aggressive behaviour by adults was evident and seems a more likely cause of dispersal, as suggested by Sadleir (1965).

Dispersal in other small mammals appears variable. Males seem to disperse more readily than females in some species -- Howard (1960) found a higher proportion of males in nine species of dispersing rodents, males dispersed more in ground squirrels (*Spermophilus*, Yeaton 1972, Michener 1972). Michener noticed both spring and autumn movements in young males. A higher proportion of males was found in dispersing rabbits (Mykytowycz 1959). By contrast Stoddart (1970) found dispersal by adult females only in a population of water voles (*Arvicola*).

Settlement and Population Levels

If social behaviour is regulating population of pikas, juvenile recruitment into the breeding population should relate to losses within the latter. The actual numbers of adults in the spring on Area I was found to increase during the first three years of the study (23 to 32 adults), however this was accompanied by a sex ratio biased towards males, with unpaired males accounting for most of the increase.

Dispersal and settlement patterns of young males could not always be related to male losses from the population, mainly because animals would move to marginal areas rather than disperse. Although young males were displaced both in late summer and the following spring, these displacements appeared insufficient to keep the total numbers of males stable. In females on the other hand, dispersal and settlement were usually related to losses of females from the adult population, or to unpaired males. Females did not settle with all males however, and as the population of males rose an increasing number remained unpaired. The result was that numbers of females varied less than the numbers of males.

Metzgar (1971) reported similar findings in *Peromyscus*, where introduced transient females settled in proportion to the number of adult females lost, whereas introduced males did not.

Recent studies of mating systems of vertebrates (Orians 1969; Downhower and Armitage 1971; Verner and Engelson 1970) emphasize the importance of female selection, and changes from monogamy to polygyny can be explained if females select males on the basis of maximising their chances of producing viable offspring. Using competition for breeding sites and then selection of these by females, the following model is proposed for pikas. Males, in order to maximise fitness, must acquire a territory of sufficient size to allow a female to breed undisturbed within it. If a male is unable to take up a large territory in the year of its birth its chances of survival would be greater if it took up a small territory, built a haypile, and waited until spring before trying to secure a larger area. If spaces are still not available the animal may be forced to take up a marginal position which is sufficient for survival but inadequate for breeding. As a final alternative it may be forced entirely from the population. In females, settlement will be associated with only those males able to provide suitable territories. Thus most marginal males will be ignored and female losses replaced directly. Occasionally a male may have a territory of sufficient size and resources to maintain two females. If competition between males is such that the territory sizes are generally reduced, a drop in female numbers could result. This could have occurred on Area I since the loss of females from the population during 1970 - 71 was high on the densest part of the slide and may have been associated with the increase in the number of males on the area at that time. Whether this loss of adult females was due to dispersal or death is not known.

In conclusion, pikas appear to have a spacing system which affects the number and location of new recruits settling into populations. Such a system, although likely to be related to the food supply in a general way, appears to place an upper limit on the breeding population each year.

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APPENDIX I

On Area IV over the winter of 1969-70 a small group of pikas, selected at random from among the marked individuals present in August 1969, had their haypiles experimentally increased by an order of magnitude greater than 100 percent. Their survival over winter was compared to the remaining marked individuals. No significant differences were found.

	Experimental group		Control group	
Adult males				
	BB	Lost	WB	Lost
	WR	Survived	BW	Lost
	WG	Survived	YR	Survived
	NW	Survived	RB	Survived
			NY	Survived
Adult Females				
	GR	Lost	WW	Lost
	KY	Lost	NN	Survived
	YG	Survived	GG	Survived
Juveniles (sexes not known)				
	RW	Lost	BY	Lost
	NG	Lost	NK	Survived
	WY	Lost	RR	Survived

APPENDIX II

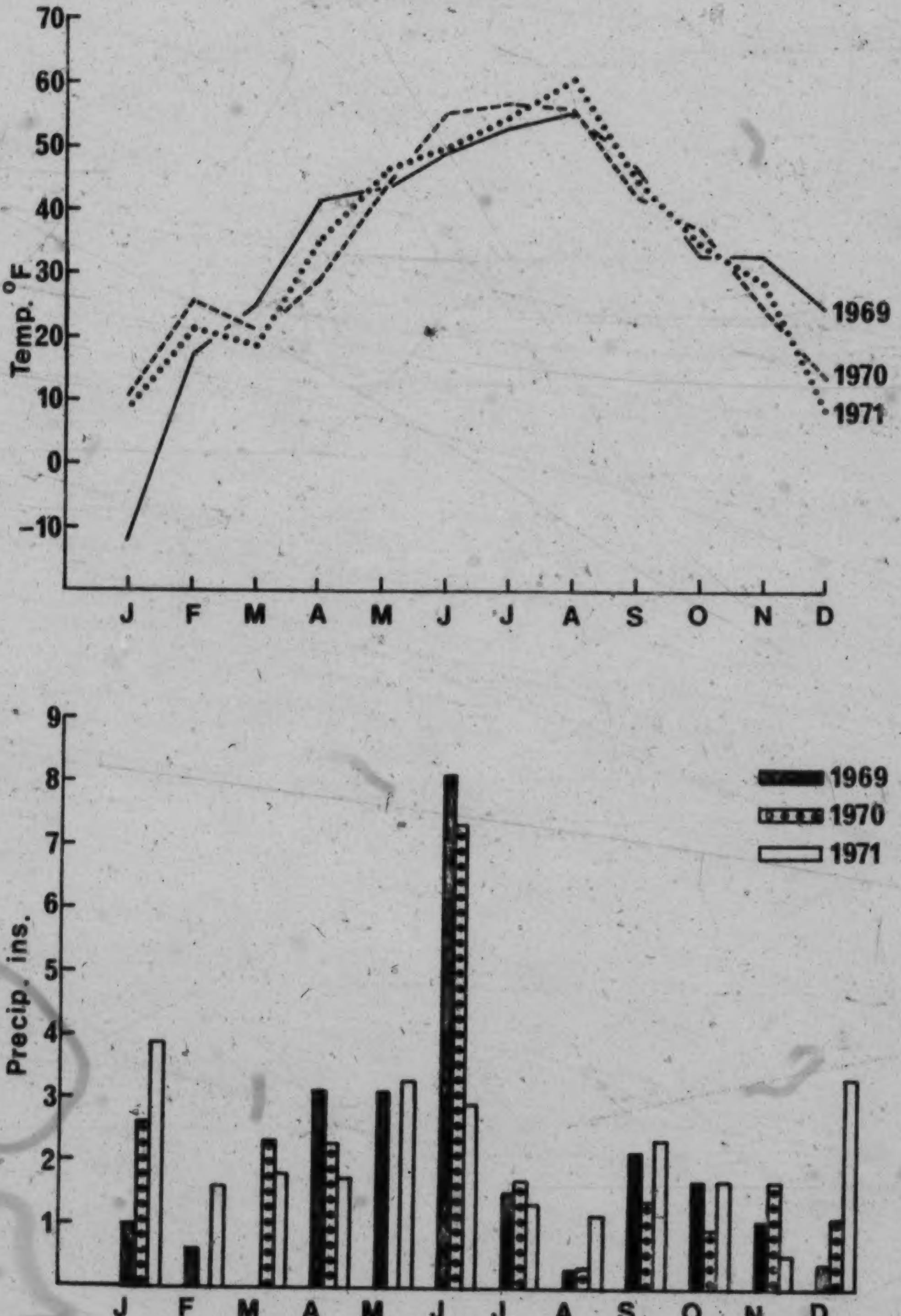

Fig. 28. Mean monthly temperatures and monthly precipitation totals from Highwood River Ranger Station in S. W. Alberta.

APPENDIX III

The following dispersal movements of pikas were recorded by J. S. Millar from his Sheep River study areas during the summers 1968 - 70.

Sex	Distance (metres)		Time of movement
Female (juv)	1st	107	Late summer
	2nd	107	?
Female (juv)		230	?
Female (juv)		104	Late summer
Female (juv)		850	?
Male (juv)		120	?
2 Females (juv)		Immigrant	Late summer
Female (juv)	1st	Immigrant	Late summer
	2nd	185	
3 Females (juv)		Transient	Late summer
Male (juv)		Transient	Late summer

3 Females - not on study area in late summer were present the following spring.